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The Podocarp-Broadleaf Forests of New Zealand *†

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Abstract

IT has long been recognised that New Zealand's mixed lowland rain forest presents an unstable pattern in which the podocarp element is in slow decline. Leonard Cockayne, who pioneered forest ecology in New Zealand, interpreted this decline in terms of a seral process. More recently John T. Holloway has offered an hypothesis based on a recent change of forest climate.

In the present paper the unstable nature of the forest pattern is further confirmed and analysed upon a structural basis by means of forest profile diagrams. Under the broadleaf forest dominance hypothesis the true nature of the present forests is presented as a vast historical fusion between an older, purely gymnospermous forest which pioneered in the recolonisation of the post-glacial landscape, and a subsequent invading dicotylous broadleaf forest which is only now gaining the ascendancy. While the present pattern stems from the post-glacial habitat readjustment, the origins of both forests can be traced back into preglacial times.

With such an interpretation it is claimed that many of the difficulties inherent in previous approaches regarding the status, classification and dynamics of podocarp-broadleaf forest, fall into proper perspective. Such forest can no longer be regarded as a single forest entity. It represents a broadleaf forest climax which is surely replacing a more ancient podocarp forest climax, remnants of which still remain mingled with the broadleaf forest. So close are the environmental requirements of both these forests that the shift from one climax to the other has been extremely prolonged and gradual. Even the broad trends have been so obscured with such a blending and fusion that today the transitional phases—the Podocarp-broadleaf forests, are accepted as the norm.

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† The term broadleaf, arising from the writings of Leonard Cockayne, has found wide popular acceptance in New Zealand. As used throughout this paper it refers to the many dicotylous hardwood trees found in association with the softwood podocarps of the mixed forests. Compare Podocarp-Mixed Hardwood forests of Holloway (1959).

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Introduction

Dr. L. Cockayne (1855–1934) contributed more than any single individual to an early understanding of New Zealand forest vegetation. His numerous papers and books appeared at a time when plant ecology itself was but a pioneer subject, while his "Vegetation of New Zealand" with two editions and a recent reprinting, has remained a classic on New Zealand forest ecology for over 30 years. In particular Cockayne may be regarded as responsible for two major concepts which have influenced most subsequent thinking and interpretation in relation to New Zealand forests. The first was that the mixed lowland evergreen forests could be classified as subtropical rain forest and the second was that a national decline in the podocarp element was evident with a corresponding rise to dominance of certain broadleaf trees, all part of a simple linear seral process.

Part I.—The Forest Pattern

Apart from the evergreen forest dominated by kauri, *Agathis australis*, which is now found only in the north of New Zealand and the typically southern *Nothofagus* beech forests, there are two additional lowland forest types which may be recognised in New Zealand. These are:

(a) Mixed evergreen forest dominated by podocarps of which the rimu, *Dacrydium cupressinum*, is the most significant. The understoreys include a host of small trees and shrubs belonging to many dicotylous broadleaf families and genera. This forest is typical for the warm, moist lowlands of the North Island, but it extends with some impoverishment of species to the far south. It is the podocarp-broadleaf forest of Cockayne in which he recognised a gymnosperm-dicot ratio which varied considerably and which McKelvey & Nicholls (1957) have currently subdivided into forest types on the basis of density of podocarp stocking.

(b) Mixed evergreen forest dominated by dicotylous trees other than *Nothofagus*. Although recognised by Cockayne and others, this forest class has as yet received scant attention in the general literature. Such forest may be dominated by *Beilschmiedia taraire* in the far north; by *B. tawa* throughout the lowlands of the North Island, and by *Weinmannia racemosa* in lower montane and South Island stations.

There is much evidence from the present dynamics and distribution of podocarps as well as residual site soils to suggest that these purely broadleaf forests have generally developed through stages when a gymnosperm element was present.

Gradations between these two forests may form an almost continuous and infinite pattern and one which overlaps into both the kauri and the beech forests. These last named are not, however, the concern of the present paper.

The forest profile series. In 1933 Davis & Richards first used the forest profile diagram for the study of tropical rain forest and the method has since found reference as a useful diagnostic approach (*vide*, Richards, Tansley & Watt, 1940; Beard, 1944). A recent review of the method is found in Robbins (1959). The present study represents its first application on a national scale for the analysis of New Zealand rain forest. It is also thought to be the first quantitative use of the method, more than 50 forest stands being investigated.

The method may be briefly described as follows: A narrow rectangular strip of forest is marked out, 200ft long and 25ft in width. All small undergrowth is cleared and the remaining trees are sketched in to scale on a graphed drawing board. The results are recorded as a profile diagram showing a forest transect in depth with details of structure and relationship of the tree layers. Full notes on the ecological and floristic composition of the sample accompanies the diagram. Profile sites are not selected at random but chosen to illustrate a representative strip which is typical of the particular forest stand.

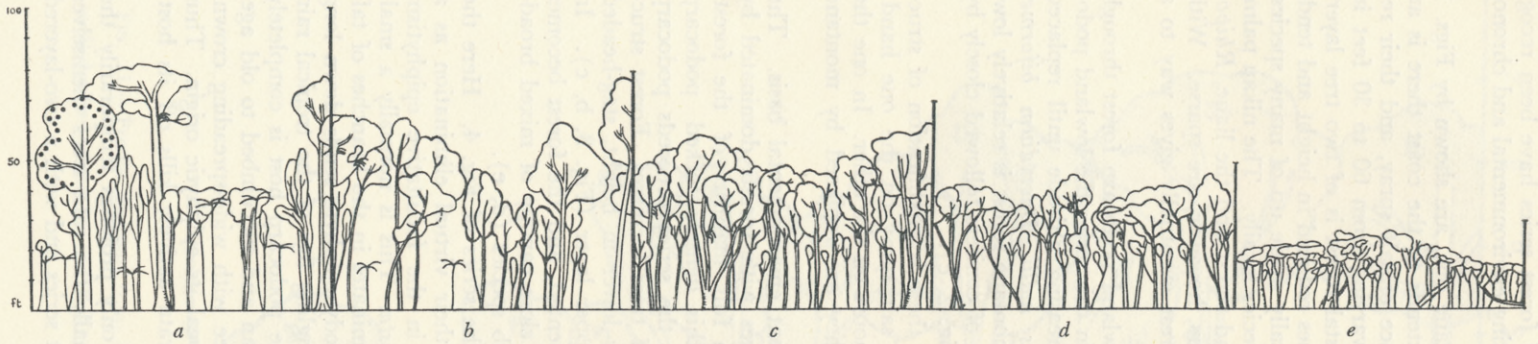

FIG. 1.—Profile diagrams of the *coastal forest series* showing elimination of podocarps (stippled) and reduction to a lower two-layered broadleaf forest; with increasing exposure to the littoral environment. Each section represents an actual 100ft x 25ft strip of forest vegetation, all within a mile or two of the coast.
a, Marlborough Sounds, Picton. b, Paraparaumu, Wellington. c, Waiwera, east coast, Auckland. d, Paraparaumu, Wellington. e, Dysoxylum forest, Stephen Island, Cook Strait, Wellington.

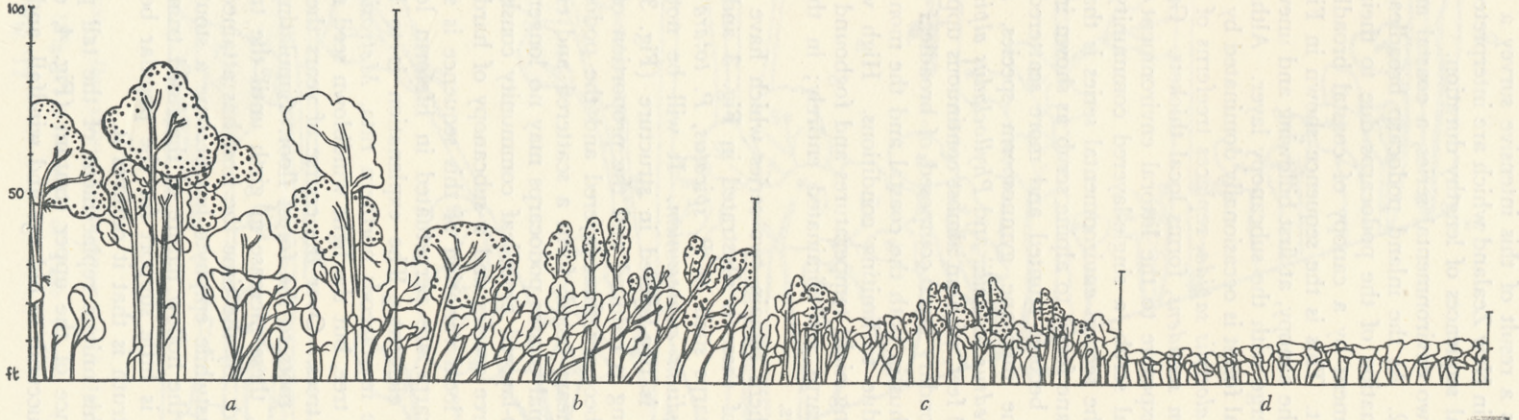

FIG. 2.—Profile diagrams of the *montane forest series* showing structural changes with increasing altitude. Gymnosperms (stippled), while changing to montane species, still retain canopy dominance. The final phase is a single-layered alpine scrub. Each section represents an actual strip of forest vegetation 100ft x 25ft.
a, Rimutaka Range, Wellington. b, Mt Cargill, Dunedin, Otago, 2,000ft a.s.l. c, Mt Egmont, Taranaki, 4,000ft. d, Mt Egmont, Taranaki, 5,000ft.

As a result of this intensive survey a number of forest series have been recognised in New Zealand which are interpreted as reflecting environmental and chronological sequences of lengthy duration.

Two environmental series, a coastal and a montane one, are shown by Figs. 1 and 2. As the inland podocarp broadleaf forest extends to the coast there is an elimination of the podocarps due to their intolerance of salt spray, and their replacement by a canopy of coastal broadleaf trees varying from 60 to 30 feet in height. This is the sequence shown in Fig. 1. Coastal forest is of two tree layers and the canopy, at first billowing and uneven, becomes reduced in height and tends to merge with the subcanopy layer. Although typically made up of many species, coastal forest is occasionally dominated by a single species locally. The nikau palm, *Rhopalostylis sapida*, replaces treeferns of the lowland forest and the liane, *Rhipogonum scandens*, forms local thickets. Ground layers, however, are sparse. With full exposure to the littoral environment coastal forest eventually gives way to a coastal scrub, a single-layered community.

The second environmental series is that from lowland podocarp forest through montane forest to alpine scrub as shown in Fig. 2. In this series the lowland podocarps become stunted and more scattered with increasing altitude until replaced by the montane gymnosperm species, *Podocarpus hallii, Dacrydium biforme, Libocedrus bidwillii* and *Phyllocladus alpina*. The montane forest is relatively low, 30–40 feet, with an almost continuous upper stratum of conifers followed closely by a secondary layer composed of broadleaf species (Fig. 2, c).

Thus in both the coastal and the montane series there is modification of structure due to limiting conditions. High winds and salt spray on the one hand; freezing night temperatures and fogbound daylight hours on the other. In one the podocarps are eliminated entirely; in the other they are replaced by montane species.

There remain two series which have no apparent environmental basis. The first of these is illustrated in Fig. 3 and commences with forests dominated by podocarps such as *P. spicatus, P. totara* and, with full maturity of the forest, *Dacrydium cupressinum*. It will be noted that this densely-stocked podocarp forest is two-layered in structure (Fig. 3, a). As the series proceeds podocarp stocking is reduced and the proportion of broadleaf trees increases. Forest structure becomes three-layered and the podocarps, now lower in height, stag-headed and heavy-boled, form a scattered and emergent upper layer (Fig. 3, b, c). In the final phases podocarps may no longer be represented, and the forest becomes a two-layered broadleaf community consisting of a close canopy of mixed broadleaf tree species and a subcanopy of hardwood scrub species (d, e).

A local variation of this sequence is shown in the series of Fig. 4. Here the podocarps are perpetuated in lifeform long after their virtual elimination as a forest element. The explanation is to be found in the facultative epiphytism of the myrtaceous northern rata, *Metrosideros robusta*. This is normally a small forest tree, but the light windblown seed readily germinates in the branches of tall rimu trees. Over the course of years the small woody epiphyte sends down long aerial roots to the forest floor. Simulating the strangling figs of the tropical rain forest, these increase in girth until the trunk of the podocarp host is completely girdled. By the time the host has attained its lifespan and succumbed to old age, the erstwhile epiphyte has become a stout forest tree with wide-spreading crown. Only the hollow nature of the fused trunk may reveal its epiphytic origin. Thus there is little support for the popular belief that rata actively kills off its host. The truth is that it outlives it.

This unique replacement of the tall podocarps only prolongs temporarily the presence of the upper stratum (Fig. 4, c, d). Finally the rata trees themselves also succumb to old age and windfall, and the forest series end with a two-layered

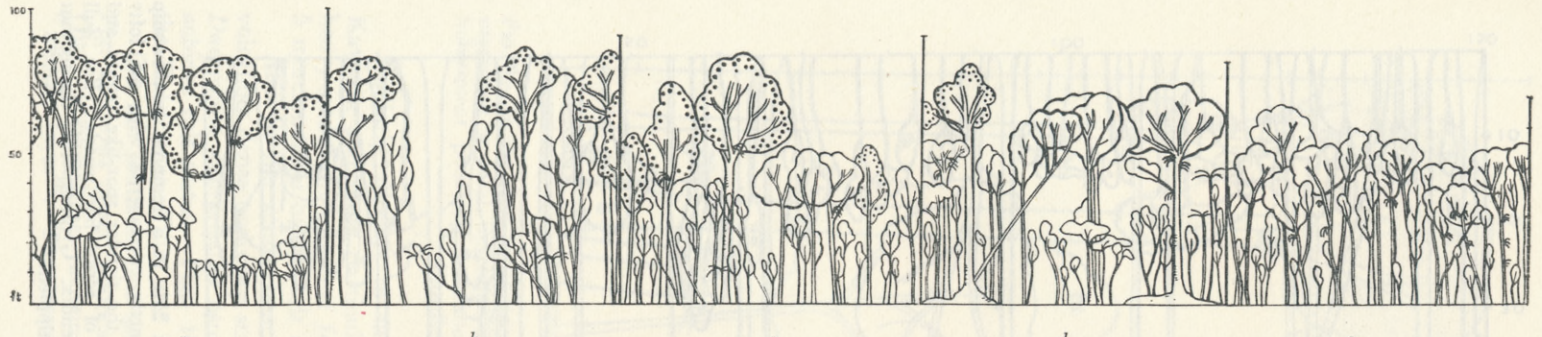

FIG. 3.—Profile diagrams of the *lowland podocarp-broadleaf forest series* showing a change from dominant podocarp forest to dominant broadleaf forest. Podocarps are stippled, and each section represents an actual 100ft x 25ft strip of forest. Note that the intermediate or mixed stages are the only three-layered forest types.
a, two-layered forest, South Taupo, Volcanic plateau. b, three-layered podocarp-broadleaf forest, Waikaremoana, Hawke's Bay. c, three-layered podocarp-broadleaf forest, Tararua Range foothills, Wellington. d, essentially broadleaf (*Beilschmiedia*) forest, New Plymouth. Taranaki Lowlands. e, Two-layered mixed broadleaf forest, Waipoua, North Auckland.

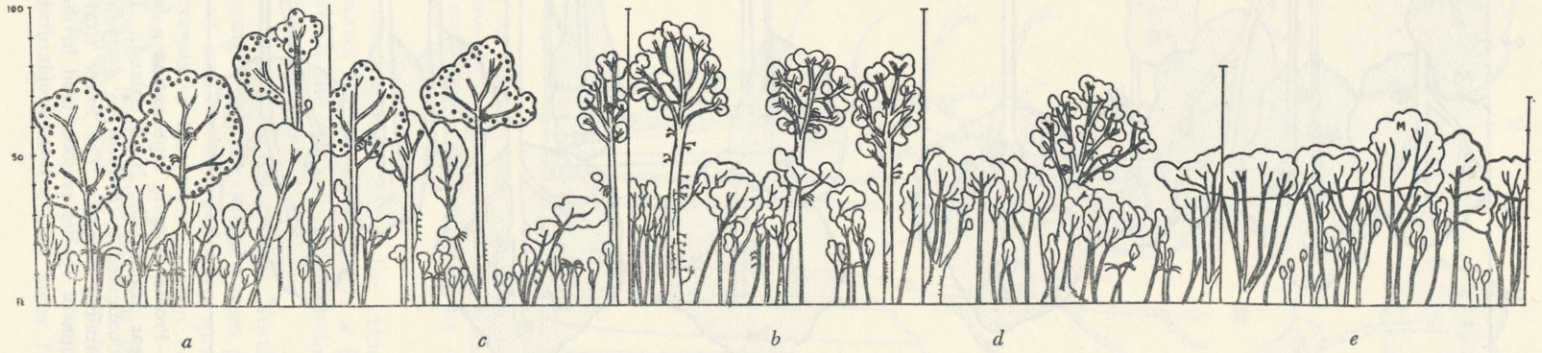

FIG. 4.—Profile diagram of the *lowland podocarp-Metrosideros-broadleaf forest series* showing changes from dominant podocarps (stippled) through *Metrosideros* (open crown emergents), to final broadleaf dominance. See text for full explanation. Each section represents an actual 100ft x 25ft strip of forest.
a, Orongorongo Valley, Wellington. b, Mixed podocarp-*Metrosideros* forest, Rimutaka Range. c, *Metrosideros* forest, Rimutaka Range, Wellington. d, Decadent *Metrosideros* forest, Mt Egmont, Taranaki. e, Broadleaf forest, Mt Egmont. Terrestrial form of *Metrosideros robusta*, marked M.

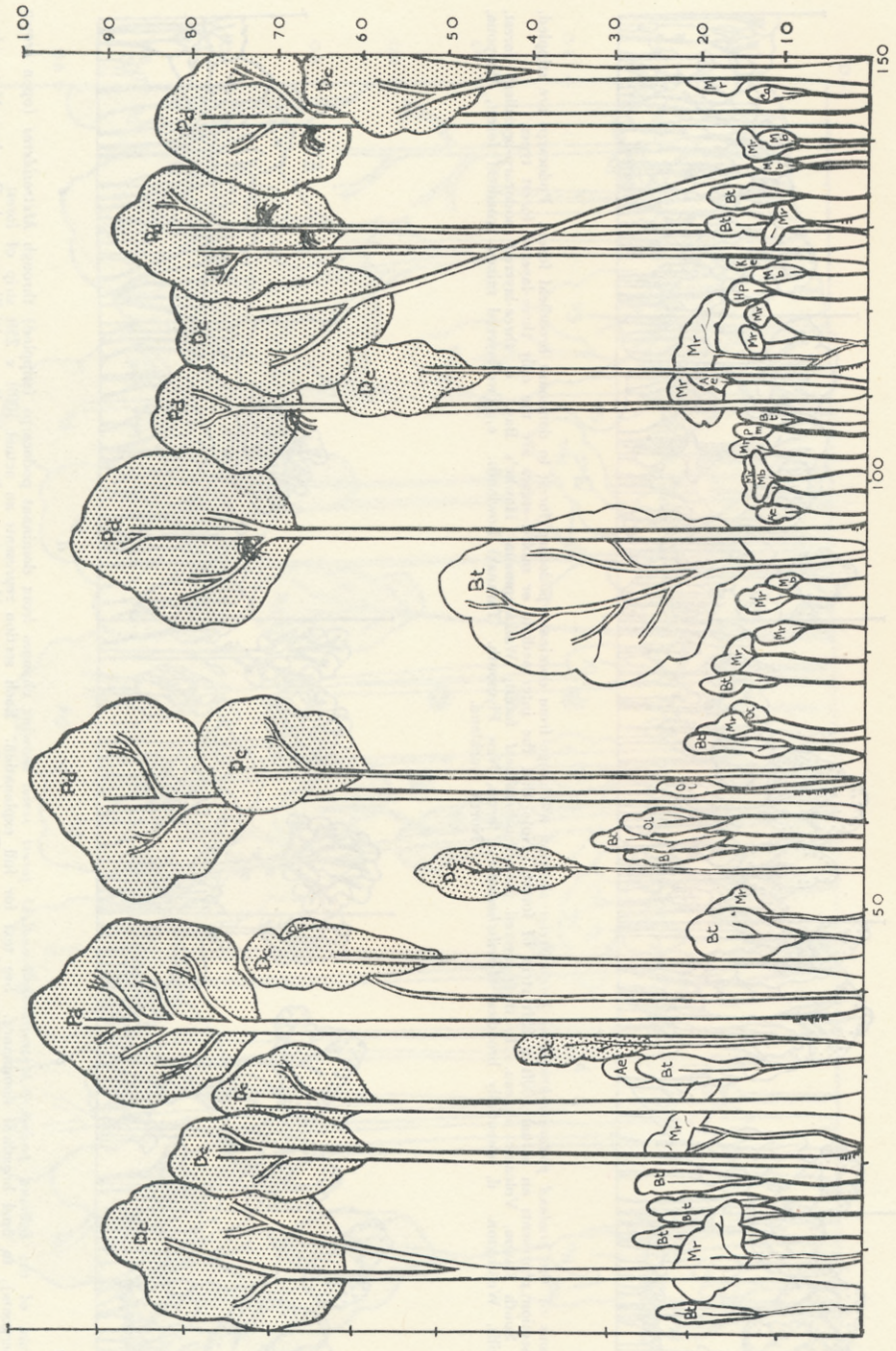

FIG. 5.—Profile diagram representing a forest strip 150ft x 25ft in a remnant semi-swamp forest near Hunterville, North Island. The forest is distinctly two-layered with the lofty canopy dominated by *Podocarpus dacrydioides* (Pd). Note the slender spar-like trunks and small terminal crowns. The lower stratum is composed of scrub hardwoods. For full explanation of species symbols used in the profiles see appendix. Gymnosperms throughout these profile diagrams have been stippled.

broadleaf forest as was the case in the series of Fig. 3. As no further tall podocarp trees are forthcoming the epiphytic phase of the rata no longer finds expression and it now reverts to terrestrial form as seen by tree "M" in Fig. 4, e.

Thus for the series illustrated by Figs. 3 and 4 there is a chronological interpretation. The series proceeds along a gradient which can only be correlated with time.

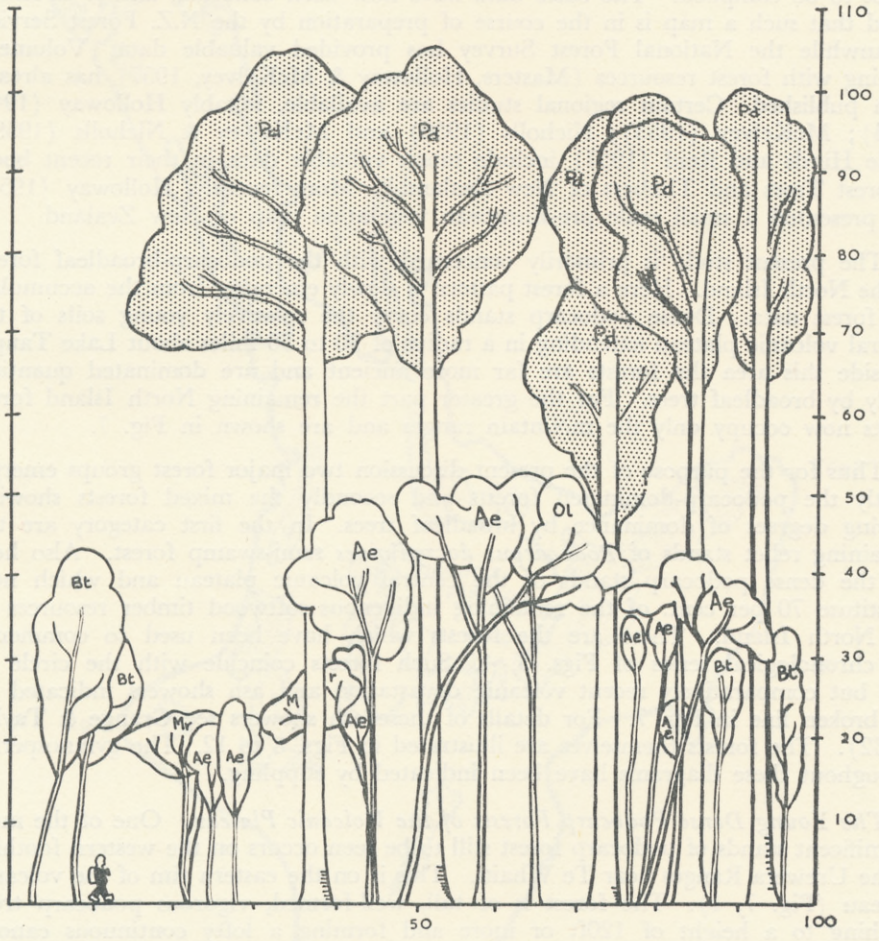

FIG. 6.—Profile diagram of a remnant semi-swamp forest near Mangaweka, North Island. Note the similarity of these forests with those shown in Figs. 10 and 11.

Finally, in this review of the forest series, is an edaphic climax which stands alone. This is the semi-swamp forest dominated by the kahikatea, *Podocarpus dacrydioides*; as shown in Figs. 5 and 6. With the possible exception of parts of Westland very few of the original large stands now remain. The profiles given here are from North Island remnants already modified by cattle trespass and drainage and marked for extinction. Uniform throughout New Zealand, these semi-swamp forests were heavily stocked with tall spar-like podocarps with slender unbranched boles and small compact crowns forming a lofty closed canopy. A "middle layer" is typically absent, the forest being two-layered, with the lowermost stratum reaching only 25 feet, sharply distinct, and composed of typical scrub

hardwood species (Pl. 1). The close resemblance of this forest both in structure and physiognomy, to the dense podocarp forest which commences the series of Fig. 3 is immediately apparent.

The Regional Forest Pattern.—Such is a broad interpretation of these lowland forests of New Zealand. Correlation with the pattern in the field becomes necessary to complete the picture. A detailed vegetation map of New Zealand is yet to be compiled. The basic data have now been collected, and it is understood that such a map is in the course of preparation by the N.Z. Forest Service. Meanwhile the National Forest Survey has provided valuable data. Volume I dealing with forest resources (Masters, Holloway & McKelvey, 1957) has already been published. Certain regional studies are available, notably Holloway (1946, 1954); McKelvey (1953); Nicholls (1956) and McKelvey & Nicholls (1959), while Hinds and Reid (1957) include much valuable data in their recent book, "Forest Trees and Timbers of New Zealand". More recently, Holloway (1959) has presented a small scale pre-European vegetation map of New Zealand.

The present study is primarily concerned with the podocarp-broadleaf forests of the North Island. Here a forest pattern is slowly emerging from the accumulating forest data. Dense podocarp stands cover the relatively young soils of the central volcanic plateau extending in a radius of 30 to 50 miles about Lake Taupo. Outside this area the forests are far more ancient and are dominated quantitatively by broadleaf trees. For the greater part the remaining North Island forest tracts now occupy only the mountain ranges and are shown in Fig. 7.

Thus for the purpose of the present discussion two major forest groups emerge. Firstly the podocarp-dominated forests and secondly the mixed forests showing varying degrees of dominance by broadleaf trees. In the first category are the remaining relict stands of *Podocarpus dacrydioides* semi-swamp forest. Also here are the dense podocarp stands of the central volcanic plateau and which now constitute 70 per cent. of the remaining indigenous softwood timber resources of the North Island. These are the forests which have been used to commence the chronological series of Figs. 3, 4. Such forests coincide with the circle of past but comparatively recent volcanic devastation and ash showers indicated by the broken line in Fig. 7. For details of these ash showers see Grange & Taylor (1932). The forests themselves are illustrated in Figs. 8 to 12. The gymnosperms throughout these diagrams have been indicated by stippling.

The Young Dense Podocarp Forests of the Volcanic Plateau. One of the most magnificent stands of podocarp forest still to be seen occurs on the western foothills of the Urewera Ranges near Te Whaiti. This is on the eastern rim of the volcanic plateau (Fig. 7, 1). The forest is of tall, well-formed, vigorous podocarp trees reaching to a height of 120ft or more and forming a lofty continuous canopy (Plate 2). Profiles of this forest are seen in Figs. 8, 9. A subcanopy of *Beilschmiedia tawa* (Bt), at 70 to 80 feet is already evident, but subsequent layers are sparse and at best represented by young tawa saplings and treeferns. There are virtually no associated hardwood scrub species, and the forest generally is poor in floristic composition, density of layers, epiphytes and lianes. These features, or the lack of them, together with the tall form of the podocarps, their heavy stocking (up to 75,000 bd ft per acre) and the total absence of *Metrosideros* as a woody epiphyte on podocarp hosts generally reflects the youthful physiognomy of this dominantly gymnosperm forest. Sited within a basin on deep pumice soils, observations on the species and age grouping of the podocarps indicate that the forest first developed with pioneer stands of *Podocarpus totara.* Dominance by *Dacrydium cupressinum* followed water consolidation of pumice particles and improvement in the edaphic conditions.

FIG. 7.—Major forest tracts of the North Island, New Zealand.
1, Urewera. 2, Kaimanawa. 3, Kakaramea. 4, Hauhangaroa. 5, Raukumara. 6, Mamaku-Rotorua. 7, Ruahine. 8, Tararua-Rimutaka. 9, Taranaki. 10, Waitakere. 11, Coromandel. 12, North Auckland.

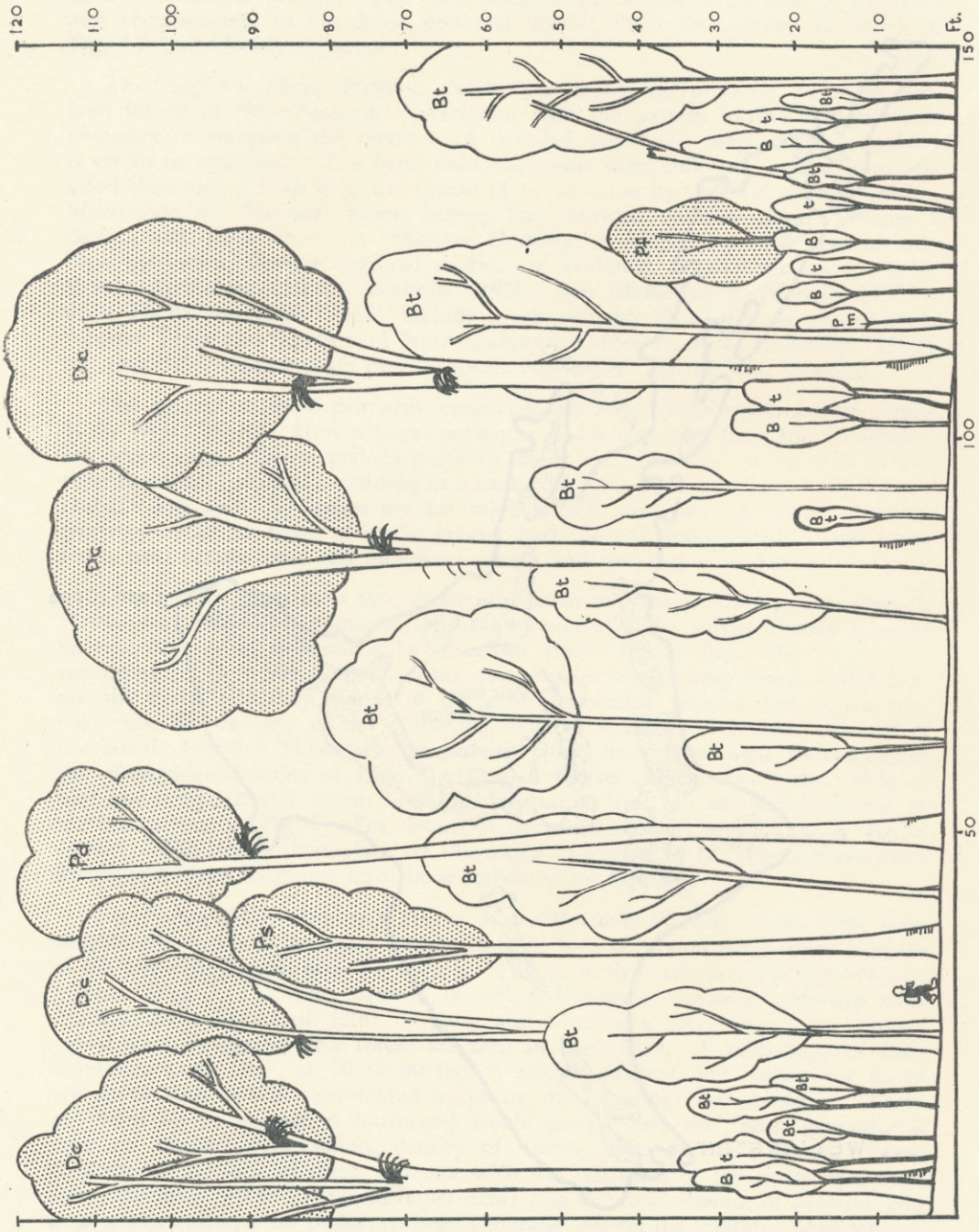

FIG. 8.—Profile diagram of tall, dense podocarp forest on the eastern boundary of the volcanic plateau, central North Island, near Te Whaiti, Urewera forest tract (Fig. 7, 1). Note the youthful *Beilschmiedia tawa* (Bt), which dominate the lower strata. This is an early stage of broadleaf invasion. The profile represents an actual strip of forest 150ft x 25ft. Shrubs below 10ft have been omitted.

FIG. 9.—In the same forest stand as Fig. 8. Note the relatively older *Podocarpus totara* (Pt) suggesting a seral development towards a dominance by *Dacrydium cupressinum* (Dc). Subsequent podocarp generations will have to regenerate under an increasing density of broadleaf trees (Bt). Note the scale figure.

Similarly, directly to the south, along the lower slopes of the Ahimanawa, Kaweka, and more particularly the Kaimanawa Ranges (Fig. 7, 2), a fringe of heavy podocarp-broadleaf forest exists in which the stocking is 35 podocarps to 5 merchantable hardwoods of broadleaf species per acre.

Also in the south, near Tokaanu and adjacent to the central North Island volcanoes dense podocarp stands occur averaging 40 to 50 podocarp trees per acre. *Dacrydium cupressinum* usually dominates but locally other podocarp species may achieve this status. Figs. 10, 11 illustrate forests of this region. They constitute the Kakaramea, Tihia and Pihanga tracts grouped as (3) in Fig. 7.

On the south-eastern slopes of Mt. Ruapehu, podocarp stocking is still high. Fig. 12 shows mixed podocarp stands with hardwoods such as *Beilschmiedia tawa* (Bt), *Weinmannia racemosa* (Wr) and *Olea lanceolata* (O1) comprising a "middle layer". The trend in older forests—i.e., those furthest away from the

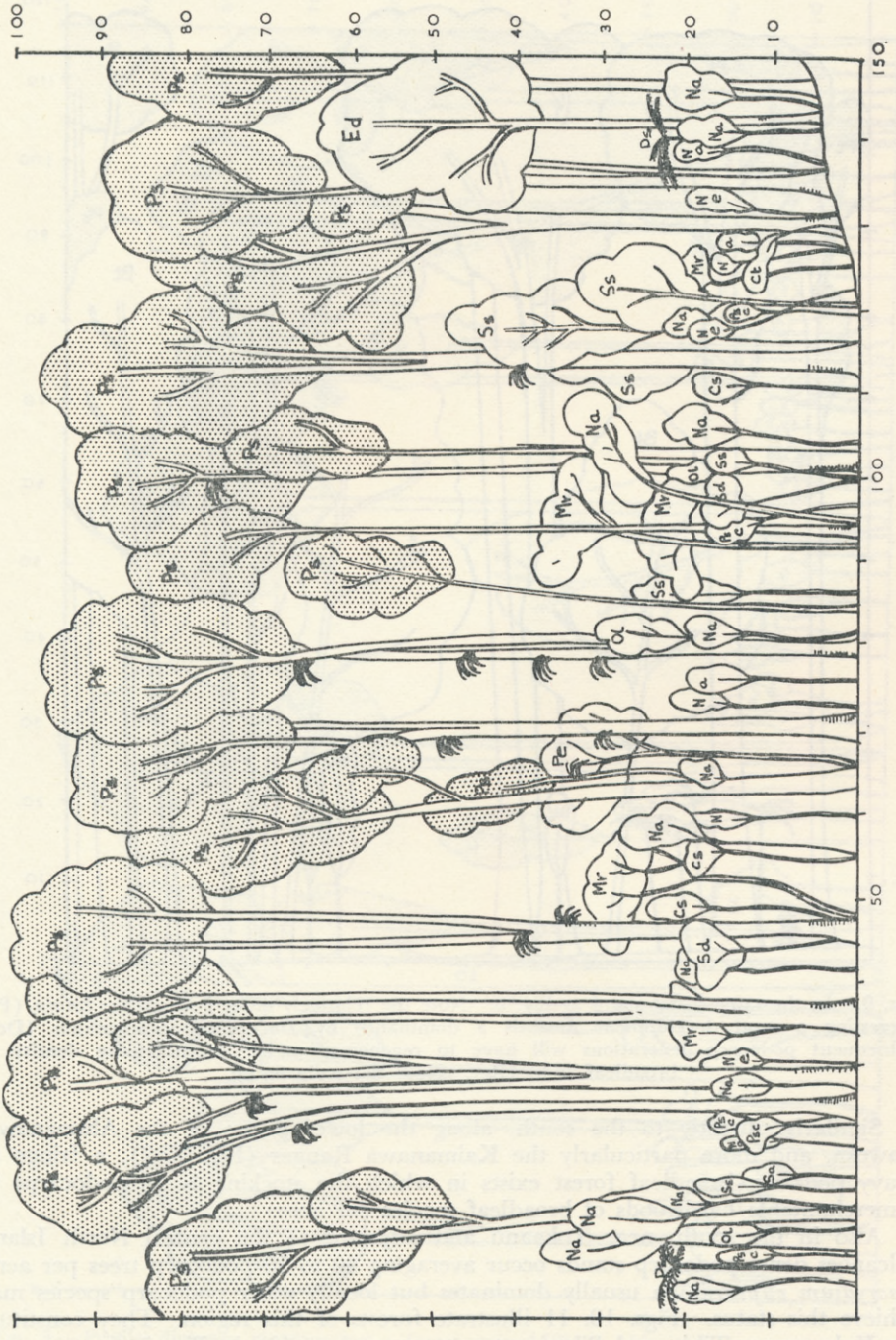

FIG. 10.—Profile diagram of a dense *Podocarpus spicatus* (Ps) stand occupying a moist site on the volcanic plateau at Kakaramea, south of Lake Taupo (Fig. 7, 3). Note the structural similarity to the semi-swamp forest shown in Figs. 5, 6. Some 20 species are represented among the associated scrub hardwoods.

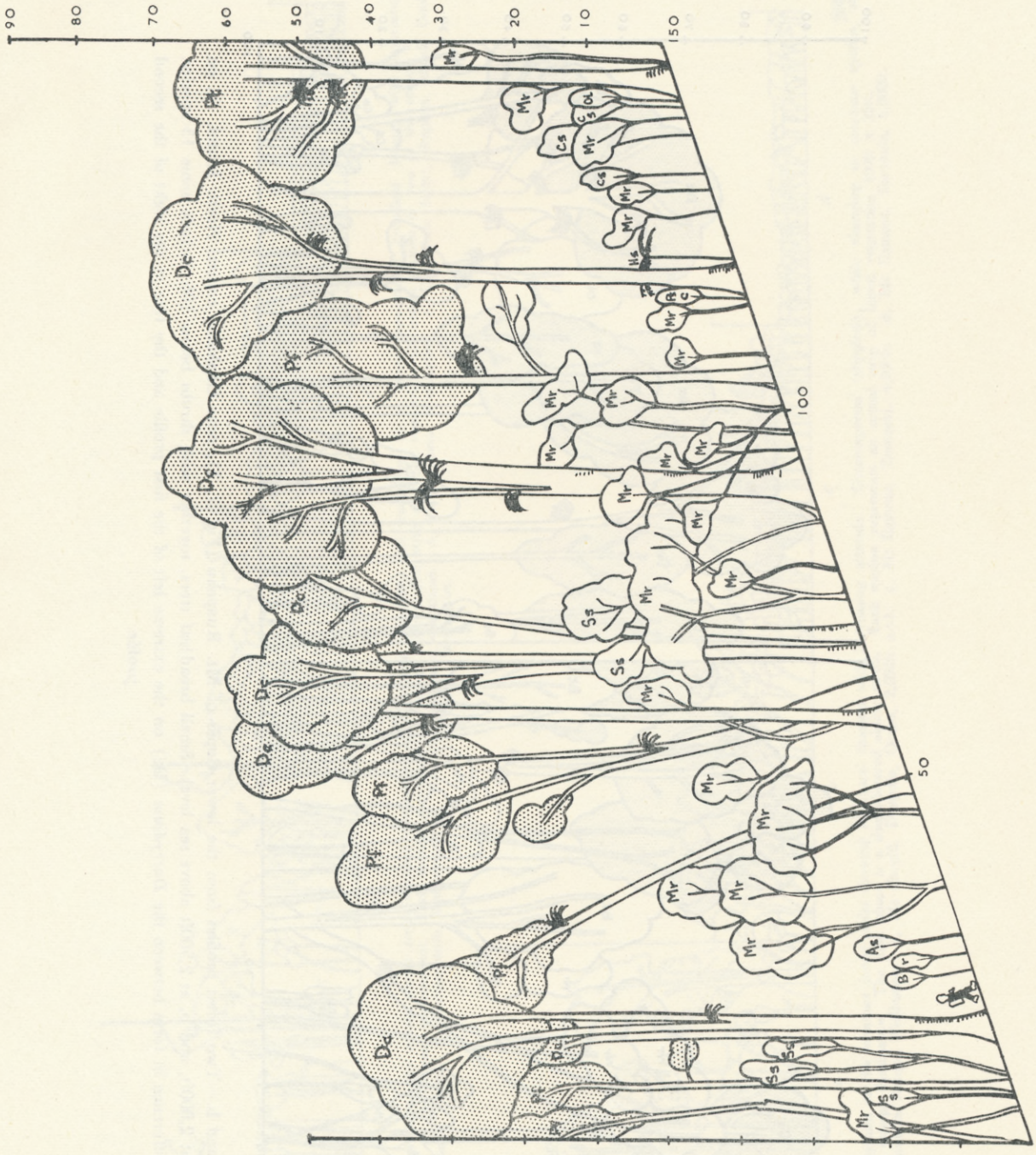

FIG. 11.—Profile diagram from heavy podocarp, *Dacrydium cupressinum* (Dc), forest on a well-drained slope in the Kakaramea tract (Fig. 7, 3), south of Lake Taupo. Compare also Fig. 12.

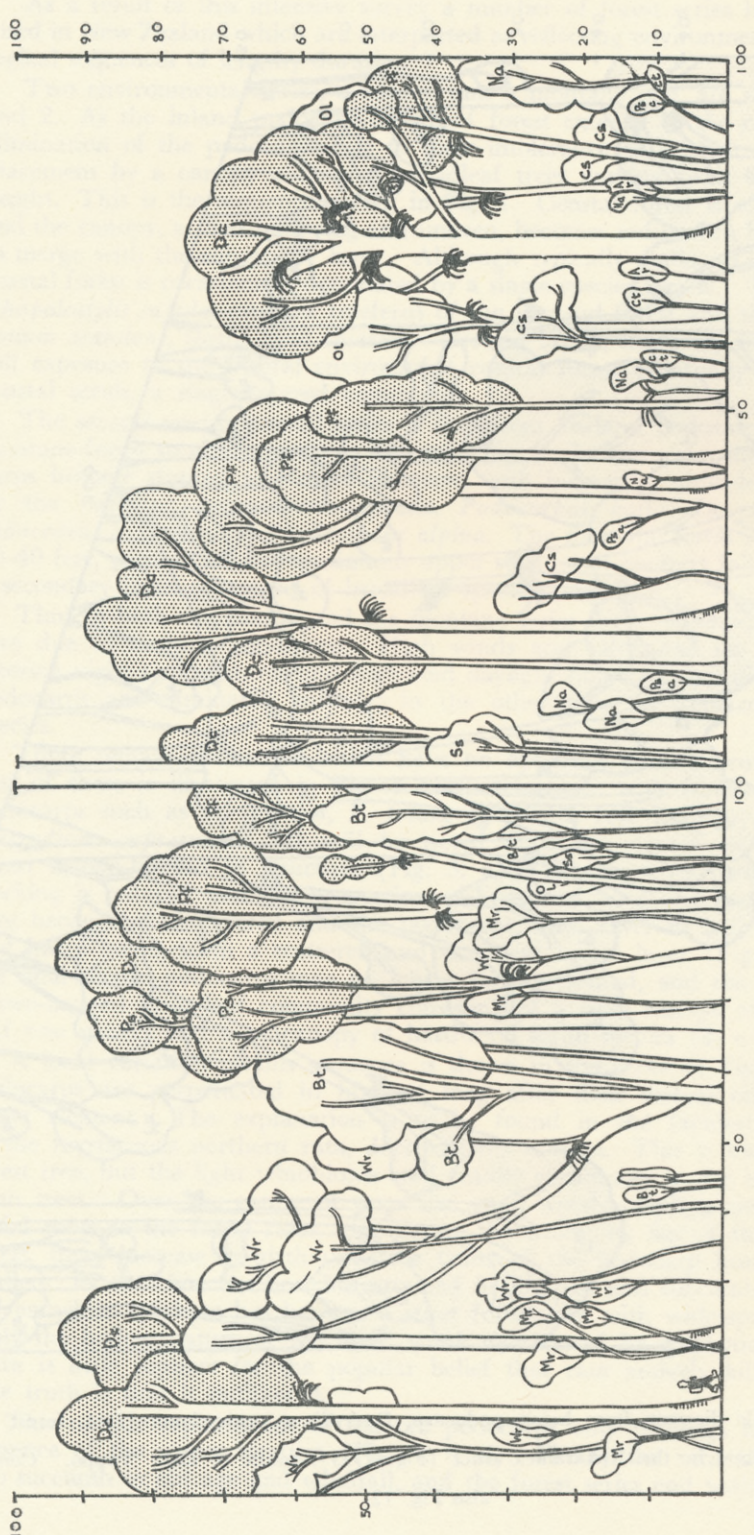

FIG. 12, a and b.—Two forest profiles from the lower slopes of Mt. Ruapehu (Fig. 7, 3), near Ohakune, central North Island. a, on the left is at 2,000ft, and b, at 2,500ft above sea level. Small broadleaf trees, together with shrubs below 10ft include some 15 species. Note the difference in form between the *Dacrydium* (Dc) on the extreme left of the first profile and the tree at the right of the second profile.

centre of the volcanic plateau, is for the podocarp trees of succeeding generations to become shorter and more heavily boled with large stag-headed spreading crowns, invariably laden with epiphytes. This is strikingly illustrated in comparing the 95ft *Dacrydium* trees of the left hand profile of Fig. 12 with the 75ft tree seen at the right of the second profile.

Immediately west of Lake Taupo, dense podocarp forest extends along the eastern fall of the Hauhangaroa and Rangitoto Ranges (Fig. 7, tract 4). These are the forests described in some detail by McKelvey (1953). The main forest of this west Taupo tract lies between 1,000 to 2,000 feet above sea level with heavy podocarp timber stands along the lake margin. Here are to be found up to 60 podocarp trees per acre, usually of medium diameter class, tall and well-formed. The canopy is at 100–120ft with *Dacrydium cupressinum* dominating. *Podocarpus spicatus* may frequent terraces and flats. Under the fairly dense podocarp canopy is a sparse broadleaf undertier at 40 to 50 feet with *Weinmannia racemosa* dominant and *Olea lanceolata* common. Present also are *Elaeocarpus dentatus* and *Quintinia acutifolia,* whilst scrub hardwoods and treeferns form an undergrowth. Locally small dense groves of sapling and pole *Beilschmiedia tawa* occur. No profiles are available, but the writer had experience in this area while with the National Forest Survey in 1946.

To complete the circle enclosing the dense youthful podocarp forests of central North Island, there remain to be mentioned the stands of dense podocarp forest which occur on the extreme southern fall of the Mamaku Plateau (Fig. 7, tract 6).

The Ancient Sparsely-stocked Podocarp Forests. Immediately outside the circle of the volcanic plateau the forests exhibit structural and floristic changes. The youthful densely-stocked podocarp forests of the central region have, where they are continuous, a sharp and distinct boundary with these older forests.

Proceeding eastwards into the Urewera tract (Fig. 7, 1), podocarp stocking falls suddenly and drastically and is represented only by scattered overmature individuals. These are invariably heavy-boled rimu trees 70 to 80 feet in height with large spreading crowns and typically supporting an advanced stage of the epiphytic northern rata. Such podocarp-Metrosideros combines are everywhere characteristic of the more ancient forests.

The main canopy is now formed by *Beilschmiedia tawa* and other broadleaf trees, while associated scrub hardwoods are rich in species, as is seen in Figs. 13, 14. On less favourable sites and at higher levels generally, *Nothofagus* beech forest prevails in this area.

In the East Cape region the main forest tract is along the 50 miles of the Raukumara Range (Fig. 7, tract 5). Podocarp broadleaf forest extends up to 3,000 feet above sea level, but as in the Urewera forests the podocarp element is scattered and overmature. Broadleaf trees dominate both quantitatively and qualitatively with such species as *Beilschmiedia tawa, Laurelia novae-zelandiae, Knightia excelsa, Elaeocarpus dentatus, Dysoxylum spectabile, Ixerba brexioides, Weinmannia racemosa* and *Olea lanceolata.* Average stocking is but 5 podocarps to 47 hardwoods per acre.

Returning to the Kaimanawa Range (tract 2 in Fig. 7), it is found that the more southerly aspects support a forest of scattered, large-diameter podocarp trees with, at the best, a stocking of 14 trees per acre.

In the same manner the western tract (Fig. 7, 4), lying over the Hauhangaroa Range becomes a sparsely stocked podocarp forest once the dense stands marginal

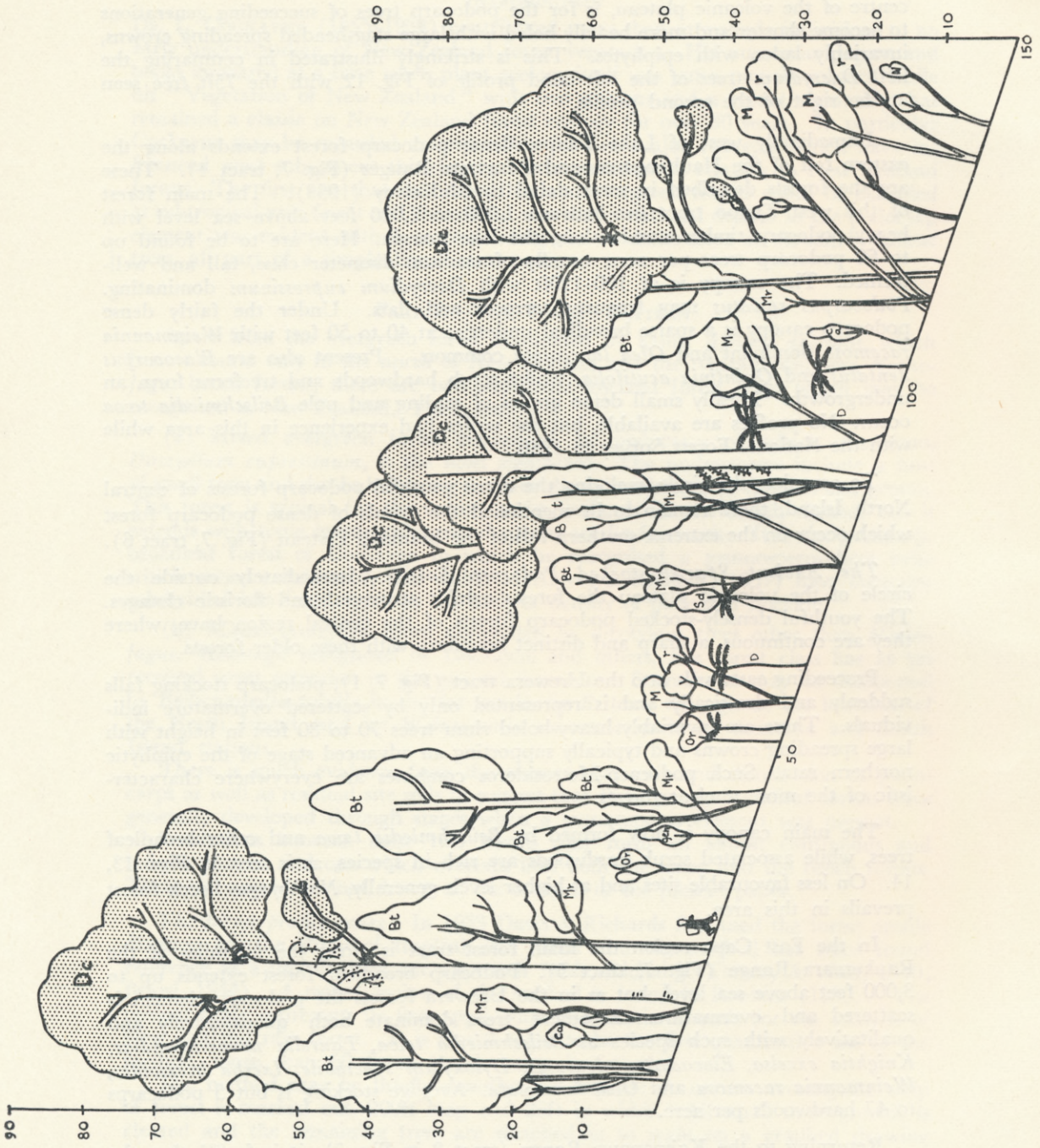

FIG. 13.—Forest profile of podocarp-broadleaf forest on the warm eastern shores of Lake Waikaremoana, Urewera tract (Fig. 7, 1). *Dacrydium* (Dc) forms a scattered emergent layer with *Beilschmiedia tawa* dominating a middle stratum. Scrub hardwoods are abundant and include some 20 species. This forest is more ancient than those shown in the preceding figures.

to Lake Taupo are traversed. Individual podocarp trees are of large diameter, commonly overmature to senile, and many are forked with large spreading crowns indicating an early suppression beneath a broadleaf canopy. Hardwood scrub species are abundant. In the extreme west of this tract the principal podocarp, *Dacrydium cupressinum*, is reduced to a few large old trees to the acre and *Metrosideros* combines are frequent. *Beilschmiedia tawa* dominates and, in association with *Elaeocarpus dentatus* and *Knightia excelsa,* often constitutes the main canopy of the forest. Tawa saplings and treeferns are abundant in the understorey. Thus from east to west across these ranges there is once again a pattern of dense podocarp forests giving way to dominantly broadleaf forest in which podocarps are present only as a scattered, stunted and decadent element.

FIG. 14.—A further forest profile from Waikaremoana. Note the many pole and ricker stages of *Beilschmiedia tawa* (Bt). Seedlings of this broadleaf tree were abundant on the floor.

In the Rotorua area two major tracts are shown (Fig. 7, 6). The western tract is that of the Mamaku Plateau, while to the east are the somewhat scattered forests of the Rotorua lakes district. The greater part of the Mamaku Plateau now supports a dense broadleaf forest in which *Beilschmiedia tawa* reaches a full development of 25 merchantable trees per acre (see Pl. 3). Only here and there old massive round-headed trees of *Metrosideros robusta* still stand in for their long vanished podocarp hosts. The adjacent Rotorua forests present a similar picture as shown by Fig. 15.

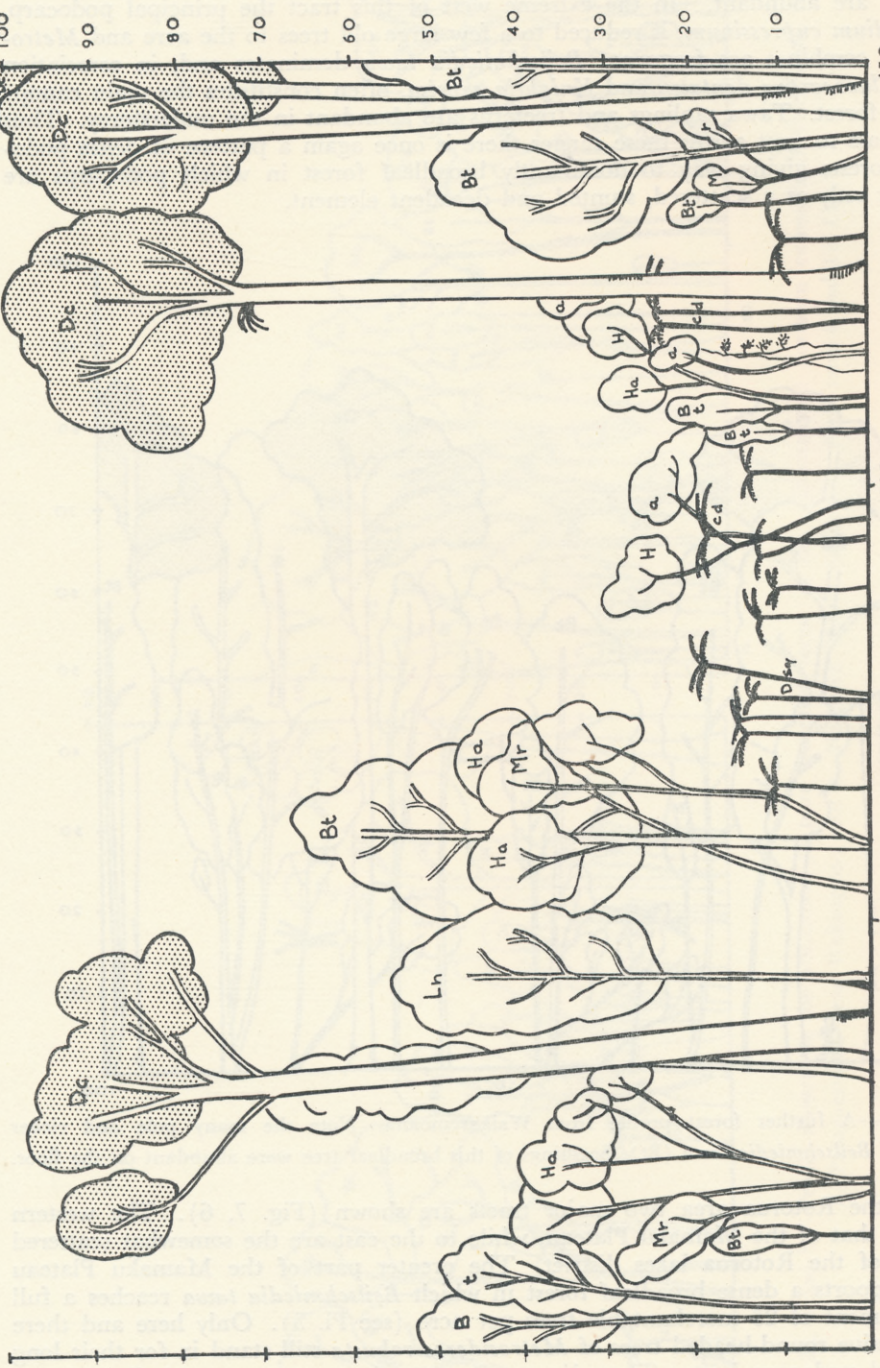

FIG. 15.—Poorly stocked podocarp forest on strongly dissected pumice country in the Rotorua Lakes district, Hongi's track. (See Fig. 7, 6.)

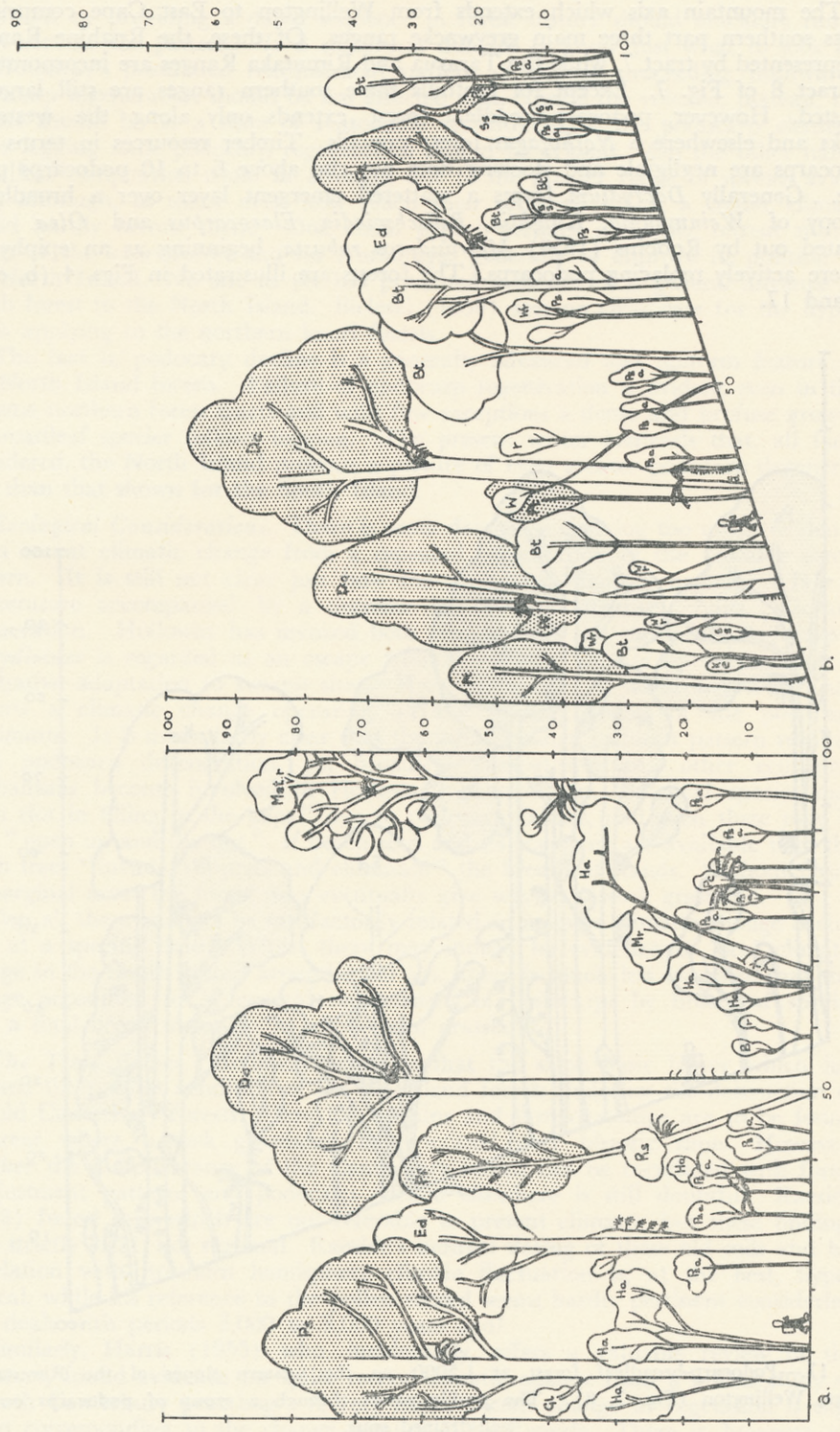

FIG. 16, a and b.—Forest profile from the southern ranges (Fig. 7, 7 and 8). The left profile illustrates an early stage in the podocarp-*Metrosideros*-broadleaf forest in the Orongorongo Valley, near Wellington. The second profile is from the western foothills of the Tararua Range, near Wellington. Here, except for the two emergent *Dacrydium* (Dc), the forest is a two-layered broadleaf forest.

The mountain axis which extends from Wellington to East Cape comprises in its southern part three main greywacke ranges. Of these, the Ruahine Range is represented by tract 7, while the Tararua and Rimutaka Ranges are incorporated in tract 8 of Fig. 7. Except for foothills these southern ranges are still largely forested. However, podocarp-broadleaf forest extends only along the western flanks and elsewhere a *Nothofagus* forest prevails. Timber resources in terms of podocarps are negligible and stocking does not rise above 6 to 10 podocarps per acre. Generally *Dacrydium* forms a scattered emergent layer over a broadleaf canopy of *Weinmannia, Knightia, Beilschmiedia, Elaeocarpus* and *Olea.* As pointed out by Robbins (1958) *Metrosideros robusta,* beginning as an epiphyte, is here actively replacing podocarps. The forests are illustrated in Figs. 4 (b, c); 16 and 17.

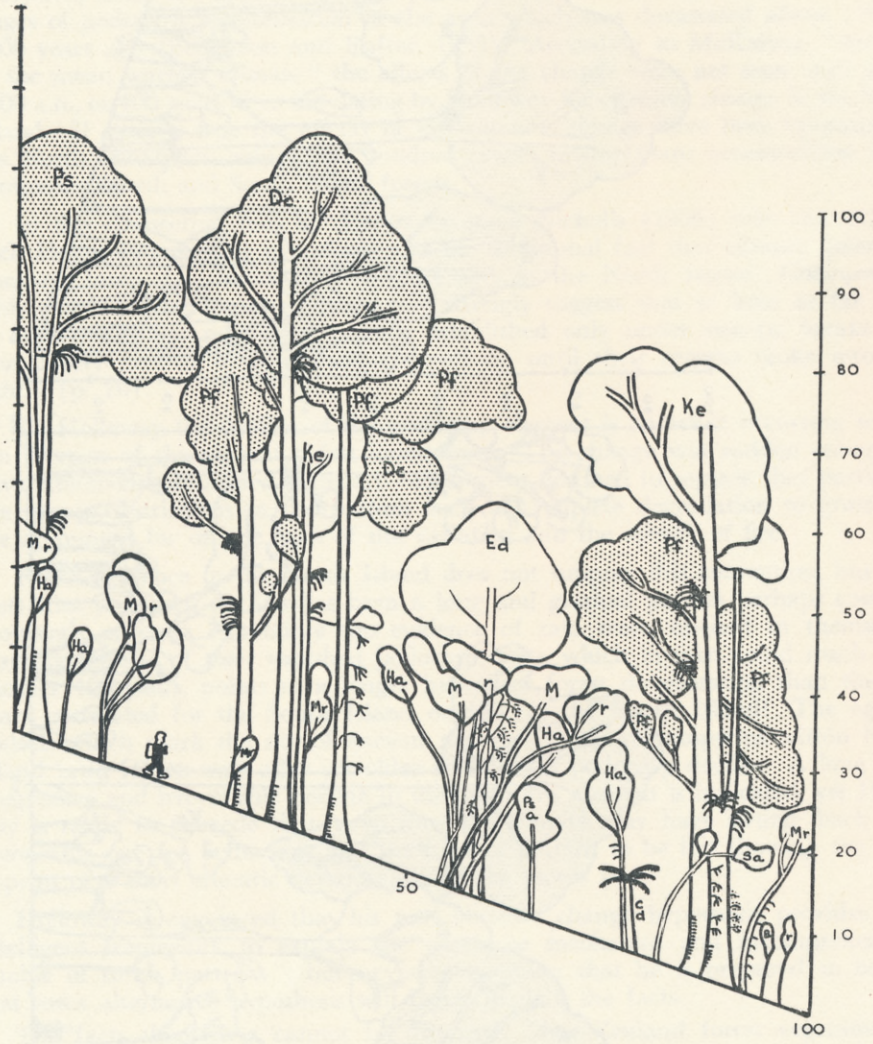

FIG. 17.—Podocarp-broadleaf forest at 1,500ft on the western slopes of the Rimutaka Range, Wellington (Fig. 7, 8). The profile passes through a group of podocarps on a well-drained spur.

The extensive but discontinuous forest tracts of the Taranaki uplands (Fig. 7, 9), extend along the west coast of the North Island. These forests have been described by Nicholls (1956) as primarily hardwood tree associations. No heavy podocarp stands exist, which is the explanation why only 4 per cent of the total is classified as merchantable forest. The forest generally is one of very scattered and emergent podocarps over a dense broadleaf canopy. Even the best type, from the foresters' viewpoint, has only three large *Dacrydium* trees and one or two *Metrosideros combines* per acre. These are emergent above the *Beilschmiedia tawa, Weinmannia racemosa, Elaeocarpus dentatus* and *Knightia excelsa,* all broadleaf species and which account for some 40 trees over 12in d.b.h. per acre. Dense groves of scrub hardwoods occur in the understorey. Most of the Dacrydium trees are from 500 to 700 years old. About one in eight is moribund, while standing dead and fallen trees are frequent.

On the eastern fringe of the Taranaki tract remnant outliers of podocarp-broadleaf forest are still to be found on the steeply dissected sandstone country west of the Wanganui River. The best stands may reach a stocking of 16 podocarps per acre, but this figure decreases sharply to an average of 5 podocarps to 10 merchantable hardwoods per acre with greater distance from Lake Taupo. Scattered podocarps, principally *Dacrydium,* but overmature, defective, or in advanced combination with *Metrosideros,* occur throughout a predominantly broadleaf forest of *Beilschmiedia, Weinmannia, Olea, Elaeocarpus* and *Knightia,* with scrub hardwoods and treeferns forming a dense understorey. Generally the Taranaki tracts show every evidence of being among the most ancient forests of the North Island. Over large parts of the region an almost pure broadleaf forest of the type shown in Fig. 3 (d) and Fig. 4 (d, e), either dominated by *Beilschmiedia tawa* or *Weinmannia racemosa,* now exists. Regeneration occurring in the wake of logging is, so far, of profuse vigorous boadleaf species.

The lower montane forest surrounding Mt. Egmont is dominated now by *Weinmannia racemosa.* A few old and senile *Dacrydium cupressinum* still stand as sentinels of the past but, windshorn and hoary with pendent lichens, these rimu trees are now succumbing to old age. Throughout this forest huge northern rata (*Metrosideros robusta*) mark the sites of long-vanished rimu hosts upon the crowns of which the windborne seeds of the epiphyte first gained its lofty stature. This dying phase of a past forest regime so well shown in these lower slopes of Mt. Egmont is even now rapidly passing. Everywhere gaps exist in the forest where wind-thrown rata trees have fallen to the ground and the forest, as seen by Fig. 18, is developing into a *Weinmannia* forest.

The forests of the north once provided the timber needed in the early settlement of New Zealand, and only small, isolated tracts now remain (Fig. 7; 10, 11, 12). Kauri forest, which is outside the scope of the present paper, may even dominate in these tracts and has a mosaic relationship with the remaining podocarp-broadleaf forest of the region. However, there are no heavy mature stands of podocarps in these northern forests and a stocking of 2 to 4 podocarp trees per acre is a good average.

In the tracts of the extreme north (12), podocarp-broadleaf forest has already reached an over-maturity beyond the interest of the timber miller. Local stands of pure broadleaf forest as illustrated in Fig. 22 (b) are to be found. It is of interest to note that here the genera *Beilschmiedia* and *Weinmannia* are both represented by exclusively northern species.

The forests of the Coromandel peninsula (tract 11) were traversed by the writer with the National Forest Survey in 1949. They do not contain any substantial podocarp timber resources. The area was early cut over for kauri and the remaining forest is on rugged topography.

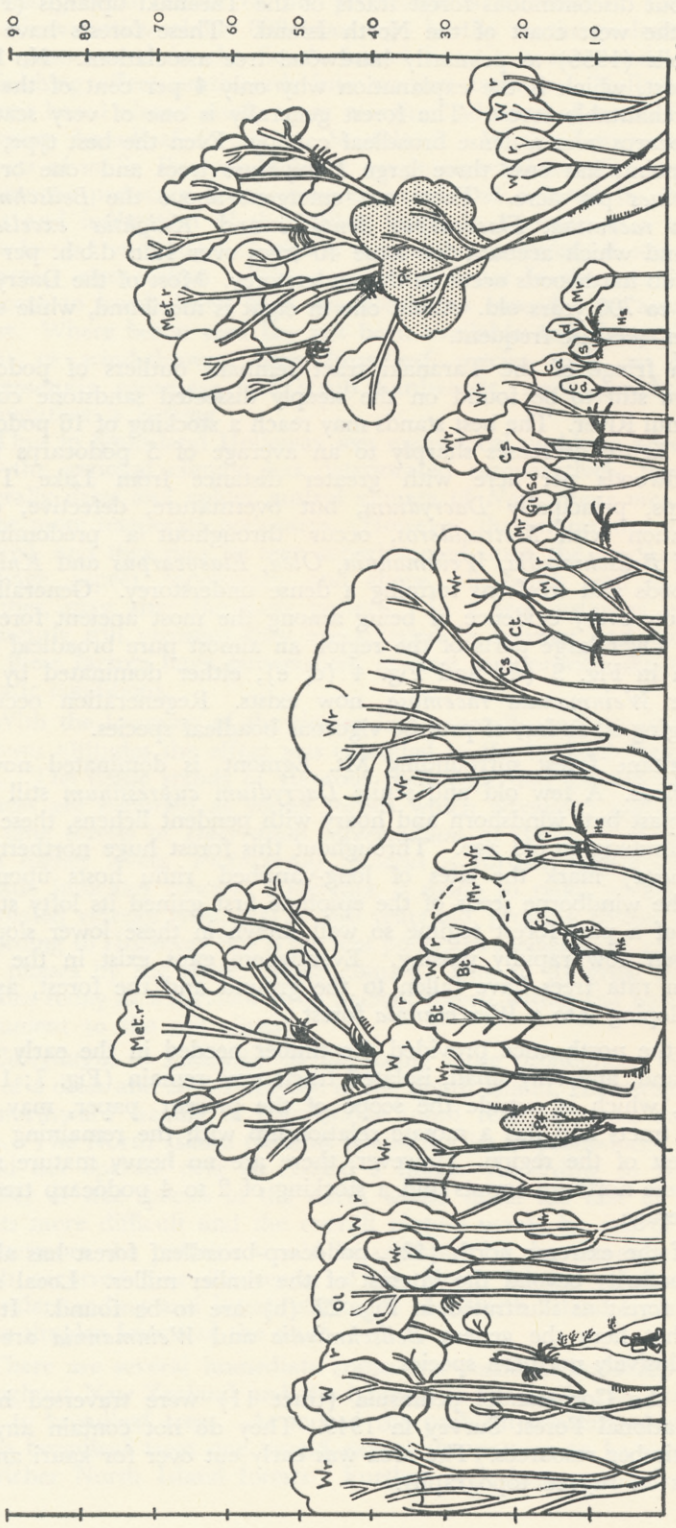

FIG. 18.—Ancient *Metrosideros* and mixed broadleaf forest on the northern slopes of Mt Egmont at 3,500ft, Taranaki tract (Fig. 7, 9). The large emergent rata trees represent the final phases of *Metrosideros*-podocarp combines. See text for full explanation. This forest is now essentially a two-layered *Weinmannia racemosa* (Wr) lower montane broadleaf forest.

According to McKelvey and Nicholls (1959) the major Northland podocarp-broadleaf forest type is of scattered *Dacrydium* and *Metrosideros* with very occasional *Podocarpus totara* emergent over a dense 40–60ft tier of mature broadleaf species, notably *Dysoxylum spectabile, Beilschmiedia taraire, B. tawa* and *Weinmannia sylvicola* with lesser representation of *Elaeocarpus, Laurelia* and *Knightia.* The ratio of the emergents is 3 to 5 trees per acre against 50 hardwood trees. In the under tiers treeferns and nikau palms are abundant, while broadleaf saplings and poles may reach a stocking of over 300 per acre. A feature of the type is the paucity of podocarp regeneration. Fig. 19 from the Waitakere tract (10 in Fig. 7), shows a forest which is already in the *Metrosideros* stage.

FIG. 19.—Podocarp-*Metrosideros* forest in the Waitakere Ranges (Fig. 7, 10). In this tract the majority of podocarps are hosts to the epiphytic rata. This profile passes through a dense group of large podocarp trees, but elsewhere the forest is predominantly of broadleaf trees.

SOUTH ISLAND PATTERN

Podocarp-broadleaf forest, albeit somewhat depleted in species, extends to Stewart Island in the south. Holloway (1954) has traced podocarp deterioration for most of the South Island and confirms here the general pattern of podocarp decline. Cook Strait notwithstanding, the forests of Marlborough Sounds in the Nelson province at 41° latitude, are but an extension of the North Island forests. *Beilschmiedia tawa* finds here its southern limit, but with an undiminished vigour.

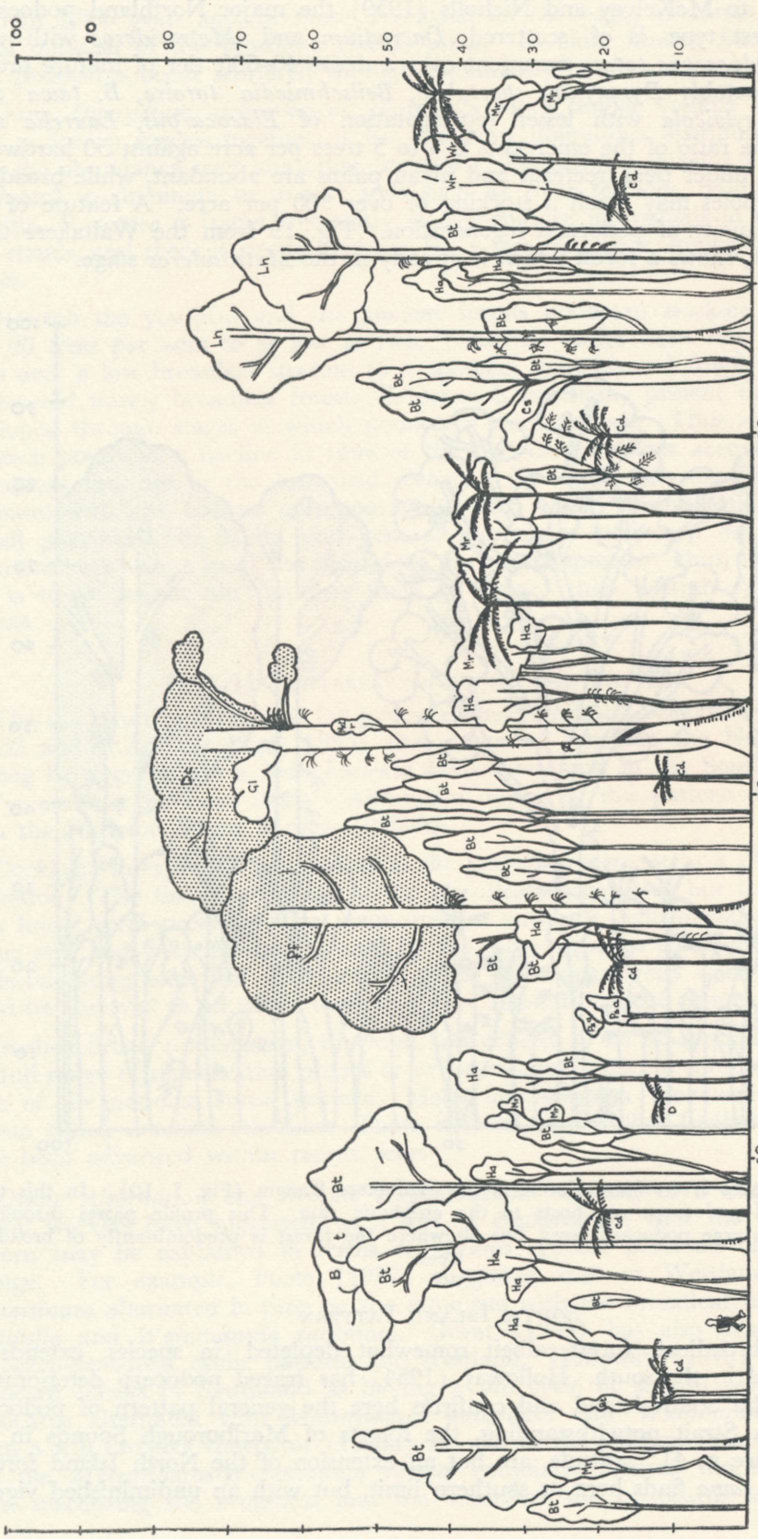

FIG. 20.—Podocarp-broadleaf forest at the southern limit for *Beilschmiedia tawa* (Bt), Marlborough Sounds, Nelson, South Island. Note the scattered podocarp species (Pf and Dc) and the vigorous growth of young tawa. *Laurelia novae-zelandiae* (Ln), is the only truly tall and buttressed broadleaf tree in New Zealand's rain forest.

This is shown in Fig. 20, a dominantly broadleaf forest with little reference to podocarps. The major tract of podocarp-broadleaf forest in the South Island, however, is that which extends along the narrow coastal plain west of the Southern Alps, an area which in the past has been severely glaciated. Here the forest again falls into two classes. There are the ancient hill forests of scattered mature *Dacrydium cupressinum, Metrosideros umbellata* and *Weinmannia racemosa* and which have long been regarded as differing in ecological status from the younger stands of dense "pole" *Dacrydium cupressinum* on the terraces. In the hill forests the large but scattered podocarps rarely reach a stocking of 8 trees to the acre, while *Dacrydium* may constitute 65 trees of d.b.h. 20–40in in the terrace forests.

These terrace forests are of tall, spar-like trees with small, compact crowns forming a close canopy at 100ft or more (Pl. 4). Fig. 21 illustrates but a rather poorly stocked example of this west coast terrace forest.

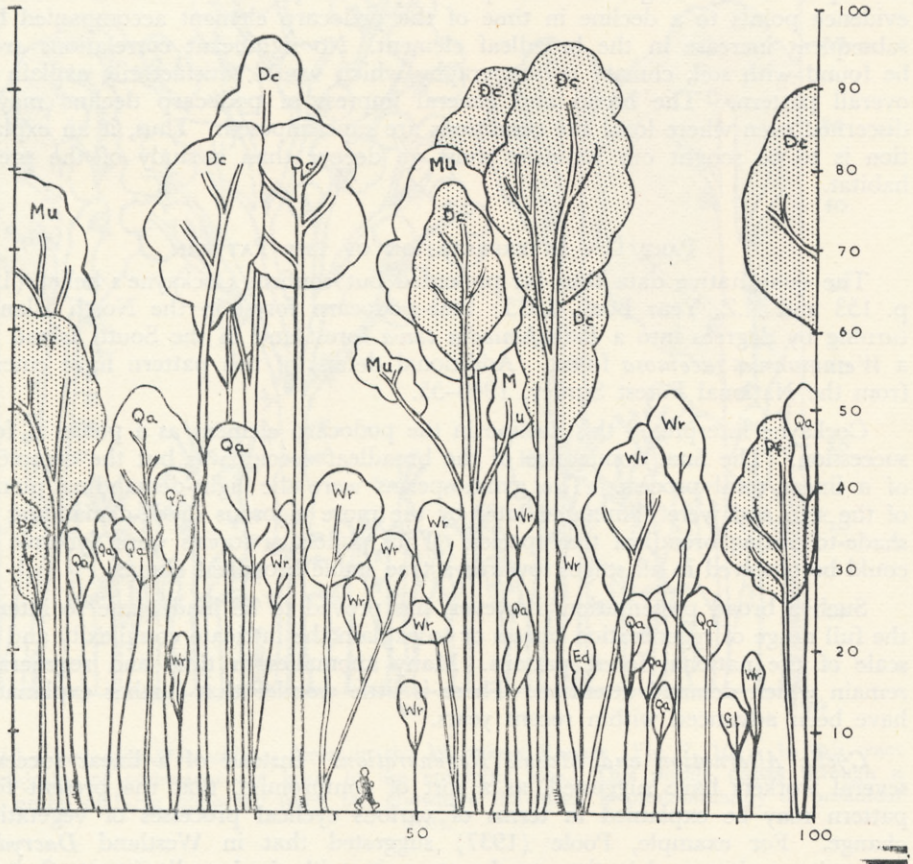

FIG. 21.—West coast terrace forest of dense tall, pole rimu, *Dacrydium cupressinum*. Profile at Lake Kaniere, Westland, South Island. These forests occupy the most strongly past glaciated area in New Zealand.

SUMMARY

The present forest pattern of New Zealand shows that the heaviest podocarp stands are always those of comparatively young forest—that is, those developed on pumice ash thrown out in the most recent eruptions from the Lake Taupo centre

less than 2,000 years ago, or those developed on the boggy moraines and fluvioglacial outwash of the Westland coastal plain. In older forests, *Dacrydium* and other podocarps occur scattered through dominantly hardwood stands.

Rimu, *Dacrydium cupressinum,* represents more timber volume than all the other podocarp species together, it has the most ubiquitous distribution and five times the abundance over any other podocarp. *Podocarpus spicatus* and *P. totara* are found to dominate on recent soils such as river terraces, basins and forest margins. *P. totara* is found frequently as over-mature individuals in mixed podocarp stands, and there is strong evidence for a seral sequence among the podocarp species.

Between the youthful and the ancient forests podocarp stocking varies from over 60 trees per acre to as low as two. Structure varies from tall, dense podocarps over a low broadleaf stratum to a complex three-layered forest and a lower two-layered purely broadleaf forest. Evidence is invariably present that these last developed through stages in which podocarps were present. Thus all cumulative evidence points to a decline in time of the podocarp element accompanied by a subsequent increase in the broadleaf element. No significant correlations are to be found with soil, climate or topography which would satisfactorily explain this overall pattern. The broad and general impress of podocarp decline may be discerned even where local site conditions are superimposed. Thus, if an explanation is to be sought our inquiries must go deeper than a study of the present habitat.

PART II.—INTERPRETATION OF THE PATTERN

The quantitative data thus far presented but confirm Cockayne's belief (1928, p. 153 and N.Z. Year Book, 1935) that podocarp forest in the North Island is turning by degrees into a *Beilschmiedia tawa* forest and in the South Island into a *Weinmannia racemosa* forest. Additional details of this pattern have emerged from the National Forest Survey, 1946–55.

Cockayne interpreted this decline in the podocarp element as a phase in forest succession. The final dominance of the broadleaf species was but the completion of a linear seral process. The gymnosperms were the light-demanding pioneers of the sere and were eliminated later by the more vigorous shade-demanding and shade-tolerating broadleaf tree species. Thus podocarp forests were dynamic and could be observed in all stages towards a true stable broadleaf climax.

Such a broad presentation, however, has proved to be inadequate to interpret the full range of regeneration phases or to explain the intricate complexity and vast scale of the national forest pattern. Many anomalies in time and regeneration remain which demand attention. There is little wonder that further explanations have been advanced within recent years.

Cyclic Alternation and Mosaic Regeneration. Instead of a linear succession several workers have suggested, as a sort of compromise, that the present forest pattern may be explained in terms of various cyclical processes of vegetational change. For example, Poole (1937) suggested that in Westland *Dacrydium cupressinum* alternated in time on the same site with the broadleaf trees *Quintinia acutifolia* and *Weinmannia racemosa.* Grant (1949) has also described similar podocarp-broadleaf cyclic patterns for Westland. Holloway (1946) regarded the podocarp forests of Southland as having a life cycle of several phases in which podocarps alternated with *Metrosideros umbellata* and *Weinmannia racemosa.* From a still broader viewpoint (1946a) he was of the opinion that the podocarps and the *Metrosideros-Weinmannia* forests conjointly formed the climax, podocarps succeeding the broadleaf and the broadleaf the podocarps in rotation on

any given area.* This defined the situation as a regular alternation of a double climax termed the " association complex ". As such it is to be clearly defined and distinguished from the concept of a mere fluctuating pattern within the forest complex.

It is this latter which has been recently expressed by Cameron (1954), who brought forward the idea of mosaic or cyclical regeneration processes to account for the composition of New Zealand's podocarp-broadleaf forests. The assumption is that because New Zealand rain forests bear a close structural and floristic resemblance to tropical rain forest the hypothesis of mosaic regeneration proposed by Aubreville (1938), and more recently discussed by Richards (1952, p. 49), will find application here.

Aubreville noted that in certain African rain forests there was a lack of effective regeneration of the existing canopy dominants. The trees destined to take their place in the upper stratum were of different species, and from this observation he propounded his hypothesis of mosaic regeneration. A regular pattern or invariable succession cycle as suggested by Watt (1947) is not implied. Rather the forest is regarded as a fluctuating patchwork, changing in time and space but remaining stable in the aggregate. Since then even the term " mosaic " has been questioned as implying definable units (Jones, 1955), whereas all that can be demonstrated is a " continuum in which the parts are in unstable equilibrium ", Hewetson (1956). Thus care should be taken to distinguish between an alternation of distinct vegetation phases (cyclic succession) and recognition of a kaleidoscopic pattern (mosaic regeneration). These are separate concepts, one implying a regular shift in the vegetation type and the other a fluctuation in floristic composition.

Holloway (1954a) emphasises that, in fact, cyclic successions involving podocarp and broadleaf phases have indeed never been fully demonstrated in New Zealand. Any amount of evidence is forthcoming for the replacement of podocarps, but there remains a gap in the cycle—the replacement of the broadleaf trees by podocarp trees. This has been endorsed by other workers, notably Nicholls (1956).

On the other hand, the hypothesis of mosaic regeneration is also untenable when applied to New Zealand rain forest. The comparison with tropical rain forest only holds as far as the regeneration failure of the existing canopy dominants. From this point there is a divergence of the facts. The " replacing " species—i.e., broadleaf trees, belong here, in the mixed forests, to the " middle " stratum. They do not give fluctuation in time and space to the upper stratum dominants as postulated by the mosaic hypothesis. These dominants, and indeed the whole upper podocarp stratum, drop out. No similar structural change occurs in the African rain forest.

Regional Climatic Change. Holloway has for some time past offered a further solution in his past climatic change hypothesis which has recently received lengthy treatment, Holloway (1954). The forests of the South Island, and in particular those of western Southland, are used to show peculiarities of forest species and forest type distribution and behaviour " explicable in terms of a hypothesis stating briefly that the forests as a whole are in an unstable condition consequent on comparatively recent changes in regional climates; and that, as a result, an active redistribution of species is in progress with resultant development of a wide range of new, though by no means stable, forest types ".

* It must be noted here that subsequently Holloway (1954, 1954a) has essentially abandoned this interpretation.

The general failure of the podocarps is therefore a consequence of recent climatic variation about 800 years ago hostile to the podocarp species. This is most pronounced in the South Island but, it is suggested, can be traced with diminishing effect northwards into warmer latitudes. Holloway's hypothesis is at present based almost solely upon marginal advance of beech forests into declining podocarp broadleaf forests in Southland. In the Longwood Range, midslope pockets of senile *Dacrydium* forest are interpreted as relict stands of a once more continuous podocarp forest now encircled and isolated by the downward movement and infiltration of the hilltop beech in response to a climatic change. At these levels the climatic change is seen as one bringing about cessation of effective podocarp regeneration. Where podocarp forest in the area has been opened up adjacent to beech forest then the beech has extended its area into the podocarp forest. Where beech seed has not been available and the podocarp forest logged, burnt or wind-thrown, then broadleaf species such as *Metrosideros lucida, Weinmannia racemosa* and scrub hardwoods grow prolifically, but podocarp regeneration is lacking.

Thus in Southland Holloway sees many local problems answered by postulating that the regional climate has deteriorated comparatively recently, favouring the generally drier and colder austral climate of *Nothofagus menziesii* at the expense of the more temperate podocarps. However, the importance of local factors is not ignored, and they may be seen superimposed upon the readjustment pattern. Soil, drainage, aspect, topography and above all, beech seed source and migration facilities, may alter the basic pattern. In a few instances where podocarps are apparently still vigorous they are situated in warmer and more favourable sites, and these factors have outweighed, at least temporarily, the onset of the adverse climatic conditions.

With the lowering of the timber line generally and the descent of beech forest to lower altitudes the effect was extended to the lowland forests of the Southland area. The dense stands of vigorous podocarps now present on the coastal gravel terraces are regarded as young forests which advanced and replaced the original bog pine forests of *Dacrydium intermedium* at the time of general forest retreat from higher levels. *Podocarpus spicatus* is further singled out as an important climatic indicator species. Reference is made to relict pockets of this forest and to isolated veteran trees, 800 to 900 years old, growing within present beech forest. According to Holloway this is the first podocarp species to be affected in its regeneration phases by the drier, cooler climate. Due to its great life-span, however, it remains today as a survivor from ancient forests within the new forests as " a living monument to the old climates ".

Correlation to Latitude. While seeing more pronounced effects of the imposition of a drier and colder climate in the South Island, Holloway, in 1954, forecasted the northward tracing of comparable forest readjustments, but on a diminishing scale. The North Island patterns would not be so pronounced as there the climate would not operate over so critical a range. According to Holloway the greater number of tree species in the north would make the task of tracing the climatic effects more difficult and the overall picture would be one of greater complexity. Furthermore the patterns would be confused by the extensive volcanic cataclysms which occurred over the centre of the North Island. Holloway concluded that an understanding and interpretation of the North Island forests was to be sought in the simpler forests of the south.

There are several immediate comments possible. Podocarp species are present throughout New Zealand and the increase in species in the North Island can only refer to broadleaf trees. As indeed the problem concerns declining gymnosperms versus broadleaf trees one would expect the pattern to be even more resolved in the richer North Island forests. Further, it is here contended that the volcanic

eruptions by providing a dated sequence in forest history should elucidate rather than confuse the pattern. It is somewhat difficult to know just what to look for in Holloway's postulated readjustment pattern of change proceeding nothwards. Podocarp regeneration should be less affected and, outside the volcanic plateau, the forests should be in a state of reasonable recruitment of the podocarp element. After logging some podocarp regeneration should be evident. On the other hand, broadleaf competition could be stronger due to the greater range of species available, although, as many even now reach their southern limits, a colder climate would hardly favour them. One could expect perhaps a further retreat northwards of the kauri forest and for *Nothofagus* generally to improve its position in the North Island. No one as yet has presented evidence of a general advance of beech forest in the North Island. Bieleski (1959) sees no clear case for the hypothesis applying to the northern kauri forests.

The fact is, podocarp decline is a generally advanced and uniform feature of the North Island forests. Failure of podocarp regeneration is evident even in the extreme northern forest tracts and with few exceptions a dense and profuse growth of broadleaf species follows logging. The present writer contends that, all facts considered, the North Island presents a picture of even greater podocarp degeneration than that shown for the South Island.

Ecological Considerations. There is some danger in deriving too much evidence for a recent climatic change from a repeated presentation of the unstable forest pattern. It is still not clear just how the postulated change—namely, a fall in temperature accompanied by a decrease in rainfall, effectively halts podocarp regeneration. Holloway has invoked both temperature and moisture. *Podocarpus dacrydioides* is regarded as an escape from the hostile climate by its capacity of facultative adaptation to swamp sites. Here, apparently, a water-logged site surmounts a climatic change operating on the seedling stages of the podocarp dominants. It is made fairly clear that the initial change in forest pattern resulted from podocarp degeneration, yet broadleaf competition and other ecological mechanisms become involved in Holloway's presentation. Boadleaf species may " run riot in filling in the gaps " due to podocarp failure, and even these may in turn " open up and die out ". If beech seed and its transport are available then the beech trees " invade, suppress and eliminate " the broadleaf stands. Without beech in marginal areas the forest may eventually give way to tussock grassland.

Can all these changes be satisfactorily related to a single climatic change occurring at a specific date? Whilst there may indeed be evidence of local climatic change in the South Island around 1200 A.D., there is much less evidence that this change accounted for a general replacement of podocarps by broadleaf species with a final beech forest or, in some cases, grassland.

The Time Factor. Holloway contends that the same basic factor which has affected the present condition of the Southland forests underlies the destruction of the old Canterbury forests. Here log remains and buried stumps are to be found in areas where tussock grasslands have existed over historic time. However, whether the disappearance of the Canterbury forests can be correlated with forest readjustment patterns and podocarp decline elsewhere is still doubtful. Raeside (1948) found soils which are not referable to present climates, but these findings were strictly local; not regional. Raeside's indirect dating of these old soils and his correlation with northern hemisphere climate fluctuation is, at the best, hypothetical, while his reference to the pollen record seems hardly pertinent considering that deals with periods 2,000 to 3,000 years ago!

Similarly, Harris (1955) who, incidentally, offers a valuable review of the literature, found evidence for quite recent climatic change from a pollen study of a North Canterbury peat bog. A very minor recent change in vegetation is suggested corresponding to the change mentioned by Raeside. There is, however, no

major change to be seen in podocarp versus beech pollen frequency and Harris emphasises that the data came from a single localised deposit and need correlation with studies over a wider area.

The evidence so far is that vegetational changes in Canterbury have been strictly local. Two factors may have brought about such changes. First, the forests appear to have been marginal in nature and dominated by *Podocarpus totara,* a pioneer on open dry sites. Thus even a minor climatic fluctuation could cause a conspicuous change. Secondly, it is generally agreed that extensive forest fires swept the area in prehistoric times.

McKelvey (1953) has commented on Holloway's hypothesis with respect to North Island forests, but only in relation to the youthful volcanic plateau forests. McKelvey holds the opinion that the postulated climatic change modified the later stages of podocarp recolonisation of the area which was devastated about 1700 to 1800 years ago (Fergusson and Rafter, 1953). According to McKelvey, "because of the mean warmer climate" the effects of the change were not seen until about 1600 A.D., or 400 years after the dating by Holloway for effective change in the South Island. If such is true the effects of the climatic change have been operating in the North Island for only a few hundred years, an important consideration when comparing North and South Island forests.

In this connection it is of interest to quote Nicholls (1956) who also accepts both Holloway's general hypothesis and the additional fact that climate deterioration was later—i.e., less than 800 years ago, in the North Island. Concurrently with this belief he found evidence to "strongly suggest that at least as far back as 1000 years ago podocarps became established only under canopy breaks and were sorely pressed by hardwood competition until their crowns broke into full light" (p. 28).

To Holloway the decline of the podocarp element is an event occurring within the lifespan of the present oldest living trees. The change was sudden enough to have effectively suppressed podocarp recruitment destined to replace that particular age group. Variations in the pattern such as complete degradation to grassland, are accounted for on the basis of site variation and the agency of fire.

Forest evidence in the North Island does not support this contention, but suggests that podocarp decline has been a long and gradual process perhaps covering thousands of years. Certainly the evidence of rata trees, ancient in themselves, marking the site of their vanished podocarp hosts, which in turn could reach back another 400 years, points to a longer history of forest deterioration than the 800 years postulated for the South Island or 400 for the North Island! The eggcup podsols which mark the site of ancient mor-producing gymnosperms within North Island tawa forests may offer yet older evidence of podocarp decline. A long term progressive and irreversible decline in the podocarp element is indicated, yet Holloway is ready to concede that even now the climate may have swung back to a favourable one for podocarps and the present pattern to be but showing the deep imprint of a short climatic deterioration in the recent past.

Holloway is convinced that his past climatic change hypothesis provides "an intelligent framework to explain the otherwise incoherent and incomprehensible jumble of forest patterns", but nevertheless states that he is prepared to believe that some alternative hypothesis will better explain the facts.

The facts themselves cannot be disputed. New Zealand forest vegetation at the present time presents a changing and complex pattern which is not referable to any simple or obvious explanation. It is the elucidation of this pattern which is the question. As Holloway declares in his final remarks, "the debate is now open".

PART III.—THE BROADLEAF FOREST DOMINANCE HYPOTHESIS

The present writer believes that the problem of elucidating the pattern of New Zealand's podocarp-broadleaf forest has a far more profound basis and one which reaches back into geologic times. The mixed forest of the present day is in reality a fusion of two forest types, both distinct in origin and history; in structure, composition and ecology.

This fusion forest is a vast unstable ecotone which can be interpreted as a shift in climax with a new order of forests arising over the entire length of the country. There is a slow and gradual rise to dominance of one forest type over another; a struggle into which one may still read something of the story of the rise to supremacy of angiosperms over gymnosperms. Only in the centre of the North Island in areas devastated by volcanic eruptions and along the glaciated west coast of the South Island has the process been retarded.

The more ancient forest type is that dominated by podocarps which had its basic origins in ancient Gondwanaland from early palaeozelandic stock. In contrast, the angiosperm forest dominated by broadleaf trees belongs to a later period and entered New Zealand as an invading group during early angiosperm migrations, and has since undergone considerable independent evolution. Upon this background was impressed the glacial period and the present-day forest pattern is derived from this climatic catastrophe.

If such contentions are correct and two distinct forests are involved, then pure stands of both these forest types should exist somewhere in New Zealand. Only thus can an ecotone be resolved.

The original podocarp forest is now in an advanced period of decline and fusion and it becomes increasingly difficult to demonstrate it as a distinct forest type with its own composition, structure and function. One must look to where it may be found in refugeum or where rejuvenated by some circumstance such as a change in the habitat. For example, the ancient gymnosperm forest may still be seen in the semi-swamp *Podocarpus dacrydioides* forests of New Zealand. These are illustrated in Figs. 5 and 6. The forest structure is two-layered with a lofty, closed canopy composed entirely of podocarps. A second stratum is formed by a low distinct layer of mixed hardwood shrubs at 15–25 feet. In virgin stands such a "ground" layer would be sparse and podocarp regeneration vigorous. However, the few remaining stands available for study are now much modified by cattle interference and drainage.

More easily demonstrated are the purely dicotylous forests. This is understandable, since they are in the ascendancy, and over large areas where time has ameliorated the site conditions, broadleaf forest has already competitively supplanted the preceding gymnosperm forest (Fig. 22).

Thus the series of Fig. 3 may now be more fully interpreted as an historical series. At first the site is occupied by an essentially pure gymnosperm forest. Such forest pioneers the site but with improvement of the edaphic conditions broadleaf tree species invade and the forest becomes a mixed podocarp-broadleaf one (Pl. 5). The various phases of this mixed forest are both numerous and prolonged, but eventually the podocarps are eliminated and the broadleaf forest established. The many intermediate stages of the series are stocked with podocarp generations which have grown up beneath a broadleaf cover. Such trees are invariably lower in stature, more massive in girth and often barely emergent above the broadleaf canopy. Occasionally an individual tree or a group may find opportunity in a gap for unrestricted growth, but these are merely adventitious (see Figs. 12, 19). With successive generations of both podocarp and broadleaf species there is a gradual shift to a purely dicotylous forest in which podocarp regeneration becomes an ever decreasing phase.

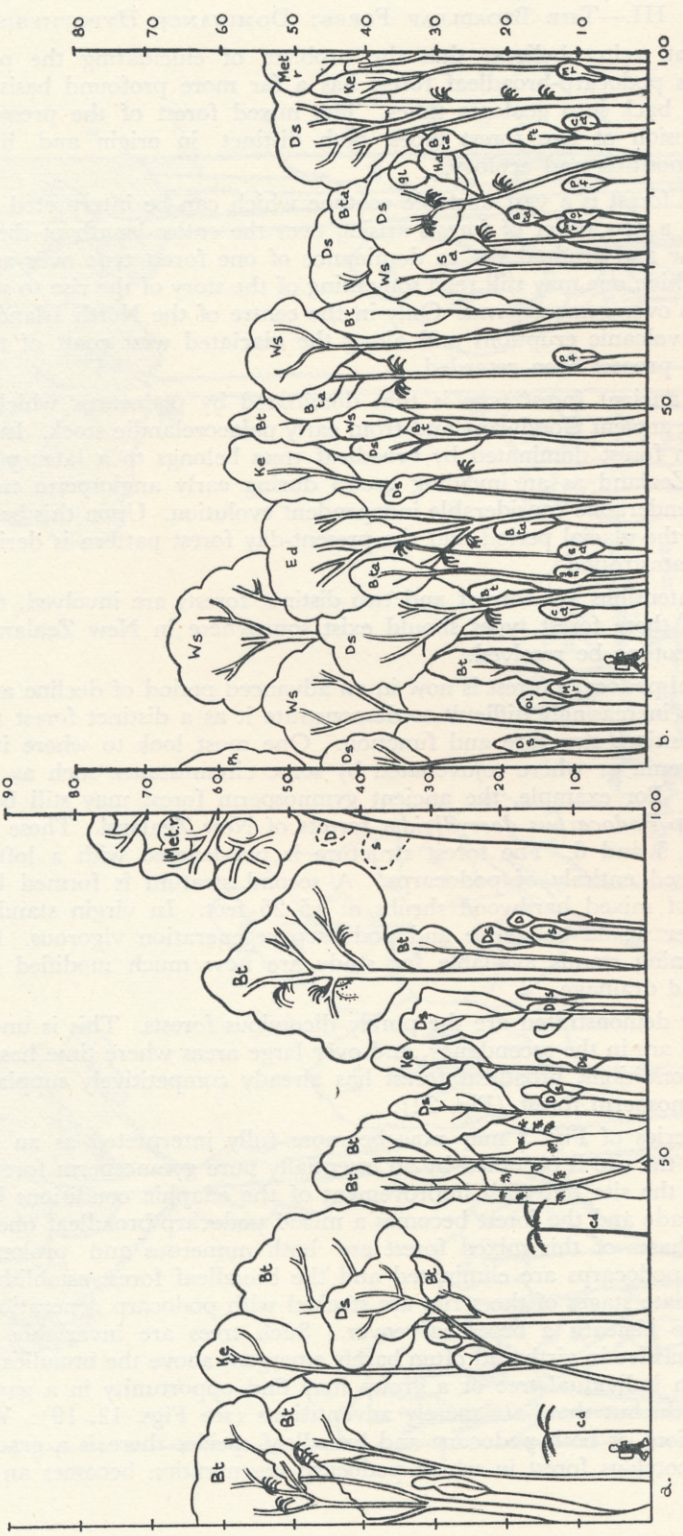

FIG. 22, a and b.—Profile illustrating the attainment of pure broadleaf forest at the southern and northern extremes of the North Island. a, Paraparaumu, near Wellington; and b, Waipoua, North Auckland. See Tracts 8 and 12, Fig. 7.

Semi-swamp kahikatea (*Podocarpus dacrydioides*) forest near Blenheim, South Island. Some *Dacrydium cupressinum* and *P. ferrugineus* are also present. Such stands represent a pure gymnosperm edaphic climax forest. They are relics of a widespread gymnosperm forest which flourished over post-glacial New Zealand.

J. H. Johns, N.Z. Forest Service.

An outlier at Puketitiri of the young dense podocarp forests of the North Island volcanic plateau. Podocarps include *Dacrydium cupressinum, Podocarpus dacrydioides* and *P. spicatus* with *P. ferrugineus*. Stocking is about 55 trees to the acre forming a continuous canopy at 100ft or more. Beneath this is a poorly developed subcanopy at 30–50ft of *Olea lanceolata*. Scrub hardwoods form an abundant ground layer. *N.Z. Forest Service.*

Broadleaf dicotylous forest in New Zealand. *Beilschmiedia tawa* dominant forest at Te Whaiti, near Rotorua, showing regeneration of sapling and pole tawa trees. Such vigorous tawa stands, however, are characteristic of the fringes of the volcanic plateau and represent recent tawa invasions. Elsewhere broadleaf forest is of mixed genera including *Elaeocarpus, Weinmannia, Olea, Knightia* and *Metrosideros.*

N.Z. Forest Service.

A South Westland rimu terrace forest of dense "pole" *Dacrydium cupressinum*. These forests were established on the tundra following the intense glaciation of the West Coast, and today remain dominant on the old glacial and river terraces as yet unchallenged by broadleaf forest. Where regeneration occurs it is of young Dacrydium.

J. H. Johns, N.Z. Forest Service.

A mixed podocarp-broadleaf forest near Taupo, central North Island. Here two forest formations have met in time and fused. Dark crowns of the present podocarp generation emerge above a canopy of broadleaved dicotylous hardwood trees. However, the slow growing podocarps are in process of gradual elimination. Each generation becomes more scattered and less vigorous; in the course of time the broadleaf angiosperm forest will take over the site.

W. J. Wilson, N.Z. Forest Service.

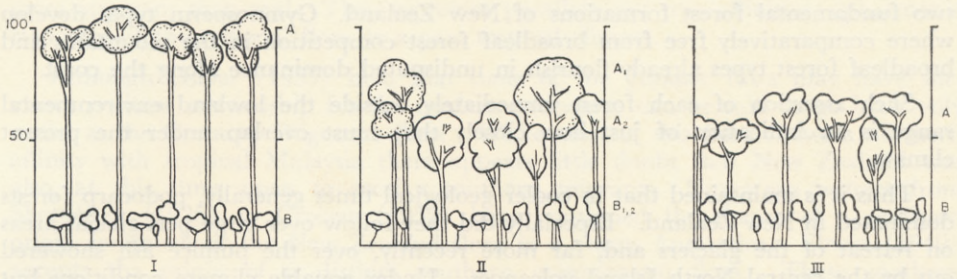

FIG. 23.—Diagram to illustrate the change in forest structure: I, two-layered podocarp forest; II, mixed three-layered podocarp-broadleaf forest; III, two-layered broadleaf forest. Podocarps are stippled.

Like the podocarp forest at the beginning of the series the final broadleaf forest is two-layered. However, there are important differences. The upper stratum is a uniform closed canopy of broadleaf trees at 60–70 feet, beneath which a second stratum follows closely. The position is analysed in Fig. 23. The tall podocarp forest of I may be considered to have an A B strata structure. In the intermediate mixed forest II there is a dispersal of the podocarp A stratum and the appearance of a "middle" stratum of broadleaf trees which here comprise the canopy beneath which is a further scrub hardwood stratum. Such forest has long been regarded as having three tree strata—i.e., A B C in structure.

With the progressive decline in the scattered podocarp emergents in the forest the position in III is reached—a two-layered broadleaf forest of A B structure. In the diagrams the layers are tagged as A_1, A_2, etc. and, from the viewpoint of recognising two forest entities as being involved, the mixed podocarp-broadleaf forest of II is not truly three-layered. It represents a transitional fusion forest in which the original podocarp forest contributes the A_1 stratum and the invading broadleaf trees the A_2 stratum. These two A strata, because of their difference in maturity height, have always been held to represent successive A and B strata of a single forest formation. When, however, the old A_1 gymnosperm stratum disappears the true independent nature of the broadleaf layer becomes evident. The so-called C stratum of the mixed forest is shown to be a mingling of the B strata from the two forests.

These changes are not merely a readjustment of a single forest element. The decline of the podocarps represents a passing of the once dominant gymnosperm forest. With its final elimination the broadleaf forest stands out independently. In 1930 Du Rietz indeed recognized this fact. He ignored the podocarps as "sometimes forming a light upper tree layer" and successfully classified New Zealand forests as *Beilschmiedia* forest, *Weinmannia* forest and *Nothofagus* forest! Until now our approach has been from the timber resources level, hence it is revealing that either podocarp stocking (McKelvey & Nicholls, 1957) or the dominant broadleaf composition (Du Rietz, 1930) can serve equally for the purpose of classification. Surely the explanation lies in the fact that we are here dealing with a fusion of two distinct forest formations!

Supporting evidence derives from the environmental series of Figs. 1 and 2. In the coastal series where podocarps are eliminated along an environmental gradient and broadleaf trees are favoured, the pure broadleaf forest, similar in structure to that ending the historic lowland series, dominates the coastal sector. On the other hand, it is the gymnosperms which better withstand the conditions in the montane series. Here the gymnosperm element is well developed and may be compared with the early podocarp phases of the historic lowland series. These extremes of forest environment acting as an ecological sieve produce, as it were, the

two fundamental forest formations of New Zealand. Gymnosperm types develop where comparatively free from broadleaf forest competition in the mountains and broadleaf forest types already flourish in undisputed dominance along the coast.

Such assertion of each forest immediately outside the lowland environmental range is an indication of just how closely they must overlap under the present climate.

Thus it is maintained that in cooler geological times generally, podocarp forests dominated in New Zealand. Especially did they follow over large peri-glacial areas on retreat of the glaciers and, far more recently, over the pumice ash showered out by the central North Island volcanoes. Under equable climate conditions but with amelioration of the edaphic factor a broadleaf forest invaded these stands. Shade tolerating dicotylous trees grew up beneath the podocarps, and these, not a changing climate, have progressively stifled the natural regeneration of the podocarp forest.

If the present podocarp element within the broadleaf forest represents the remnants of a preceding gymnosperm forest then the present ubiquitous distribution of *Dacrydium cupressinum* should be evidence that dense podocarp forests were, in the immediate past, both general and widespread. Thus the present writer cannot agree with Nicholls (1956, p. 31), that "podocarps were never more numerous than they are now, but they grew with greater vigour and therefore re-establishment was successful even where hardwoods were more abundant."

Forest Ecology. As with any forest pattern hypothesis, consideration must be given to the ecological mechanism of the changing pattern. The podocarp forest of the central volcanic plateau offers an historic experiment on a vast scale. According to C14 dating (Fergusson and Rafter, 1953), the last destructive North Island eruption occurred about 250 A.D., and thus a forest area of hundreds of square miles has been recolonised over the past 1700 years.

At first the skeletal pumice soils would have supported a scrub-heath vegetation. Soon, however, forest species would enter. McKelvey (1953) sees, for the West Taupo region, a progressive forest colonisation from the undamaged peripheral forests back towards the centre of the eruption. Closely adjacent to the old forests on the outer perimeter of the area of ash showers where the effects of the eruption were less, are podocarp forests in which McKelvey considers the present trees represent a third or fourth generation. Ring counts of large trees here show an age of 700 years. The stocking is scattered and there is a high proportion of broadleaf species with *Knightia, Quintinia* and *Beilschmiedia* dominating.

On the other hand, the forests nearest to the original centre of destruction show dense stands of podocarps averaging 400 years in age. These are regarded as first crop trees. Only a few broadleaf species are found—i.e., *Weinmannia, Elaeocarpus* and *Olea*, and even these are sparsely represented. Thus a colonising sequence is discernible—first, pure podocarps, then increasing association and dominance of broadleaf trees. McKelvey holds the opinion that a climatic change was imposed after the initial stages which reduced the aggressiveness of the podocarps and the initiative was then taken over by the broadleaf species.

Under the broadleaf forest dominance hypothesis, however, the sequence is between two distinct forests. The site is first occupied by a purely gymnospermous forest. A fact which has been often obscured is that this podocarp forest has its own seral phases. Pioneers such as *Podocarpus totara* and *P. spicatus* are followed by a dominance of Dacrydium, (see Figs. 9, 10, 11). The change to broadleaf forest is one where one community replaces another, a process along the lines of Watt's (1947) "plant pattern and process" hypothesis and Scurfield's (1956) ideas on a build up in habitat potential.

Chavasse (1954) gives some interesting data regarding podocarp regeneration. Stump analysis in a Westland forest revealed that there was a wide variation in tree age in what would appear superficially to be an even-aged stand.

Further observations (pers. comm.) are that *Dacrydium* mortality in a Westland podocarp forest lies between 4 and 5 trees per century per acre. Mortality commences after 500 years to 1,000 years with a mean life-span for *Dacrydium* of 670 years. At these figures replacement of the stand would cover a period of 435 to 545 years. When there is a broadleaf canopy at 60ft it may take 200 years for the suppressed but shade-tolerating *Dacrydium* to pierce this, and it may be thus up to 250 years of age before seed-bearing commences.

According to Chavasse further study should be made of this broadleaf tier in the mixed forest. He had observed that the broadleaf trees commonly occur in dense groves which later gradually thin out and become open-canopied and scattered. The rotation of these broadleaf groves may be comparatively short, say 200-300 years, in comparison to the full gymnosperm life-span which is two or three times as long. *Dacrydium* seedlings may become established in the stagnating broadleaf group and thus have an advantage when these trees die off and before further broadleaf competitors succeed. This may thus offer a temporary mechanism for the apparent successful re-establishment and maintenance of individual podocarps within the forest. It would certainly explain why the elimination of podocarps from the forest is so prolonged a phase and no doubt has given rise to theories of cyclic alternation.

The long struggle is not then due to climatic factors but to complex interrelations of differences in growth-rate, life-span and maturity heights of the individuals. Basically it is a matter of competition. On this contention one might maintain that the even greater decline of podocarps in the ancient North Island forests compared to the South Island, is related to the greater broadleaf competition found here. For many years it has been observed that podocarps are frequently grouped along ridges. It is significant that broadleaf growth is less here and thus there is evidence that the whole pattern of podocarp distribution and regeneration in the mixed forest is to be related to the density of the broadleaf growth.

The dense podocarp stands of the volcanic plateau may be regarded, as it were, as a clearing in the forest which allowed rejuvenation of the gymnosperm forest. Podocarps are typically pioneers and adapted to single dominant communities. Although extremely site tolerant their biological tolerance is poor. The broadleaf forest has a wider range of collective tolerance by virtue of its many species, but it is not so well adapted to prisere conditions. As an ecological entity it represents a forest with more vigorous growth rate, seed production and dispersal capacity; a forest which under favourable conditions has more autecological potential. In this must lie the reason for its final supremacy over the pioneer post-glacial podocarp forest.

The process is clearly illustrated in the central podocarp forests. The whole ecological balance of the initial gymnosperm forest is upset with the increasing density of the broadleaf invaders. The tall podocarp canopy breaks up and replacement is inadequate due to the fact that all regeneration must now take place beneath a new intermediate broadleaf stratum. Such young podocarp recruits must grow for a measurably longer time before they penetrate this broadleaf canopy. The tall and spar-like podocarp trees which regenerate within the original podocarp forest, as still evident in the relict semi-swamp *Podocarpus dacrydioides* forests are no longer to be seen. They become stunted, heavy-crowned senile individuals with long-delayed seeding capacity. Thus, with the increasing dominance of the broadleaf forest species, podocarp recruitment is stifled and eventually eliminated. The process is so gradual, however, that the replacing broadleaf trees have long been

accepted as community associates whereas in truth they are the aggressive invaders of another forest regime. The full details of their advance, and they are many, must await further research.

Forest Regeneration. Unfortunately the history of forest regeneration in New Zealand is either lacking or the time is still too short for any conclusions to be reached. Evidence is accumulating that when the podocarp-broadleaf forest is removed by milling or firing and the area left to regenerate it does so directly into broadleaf forest. McKelvey (1958) cites examples of old Maori burns which have been recolonised by broadleaf forest while Nicholls (1956) describes an area of several thousands of acres in Taranaki where the forest was destroyed by fire some 200 years ago. Here the present secondary forest is of dense *Beilschmiedia tawa.* Hardwood poles per acre number: *Beilschmiedia* 180, *Knightia* 50, *Elaeocarpus* 20 and *Olea* 10. Young podocarps are only 3 to 4 per acre. Croker (1953), studied the youthful tawa forest of the western Hutt hills, near Wellington. She concluded that it was a maturing climax developed directly after destruction of the original podocarp-broadleaf forest. Similarly Nicholls (1959) finds no podocarp regeneration over the forest areas which were lightly destroyed by the Tarawera eruptions of 80 years ago.

However, instances of dense regrowth of podocarps are not lacking (see McKelvey & Nicholls, 1959, p. 36; Chevasse, 1959) and there is no doubt that such cases have confused the issue in the past. If these are regarded as exceptions, explicable on local site conditions, then the whole question of lowland forest regeneration in New Zealand, for so long a puzzling and controversial subject, becomes clarified. Podocarps will regenerate freely and copiously when given the opportunity (see particularly Westland), but in the majority of situations they have no true future in New Zealand's forest communities. On the other hand broadleaf forest has, in itself, a clear seral history not necessarily linked with podocarps; one showing a succession of broadleaf species leading to a climax hardwood forest. In this forest a few podocarp species, in particular *Podocarpus ferrugineus,* may become adaptively integrated in the same way as a few podocarps remain in the lowland rain forests of the tropics. The podocarp climax remains as a relict in the sense of Clements (1934): "a community or fragment of one which has survived some important change often to become in appearance an integral part of the existing vegetation".

The Development of the Flora. The broadleaf forest dominance hypothesis demands a consideration of the development of the New Zealand flora and the remote forest history. The far-reaching effects of the glacial and post-glacial periods, acting upon an assemblage of plants of different origins and tolerances cannot be underestimated. As Harris (1950), points out, we have thus all the more reason to consider parentage and former environments in order to understand adjustments to contemporary conditions. The great importance of the historical approach in the study of New Zealand forest vegetation has been strongly emphasised by Cockayne. In the present forest flora he recognised elements belonging to two major groups. There was a temperate group comprising ancient palaeozelandic and subantarctic elements during the Jurassic to early Cretaceous. Land extensions to the north then enabled the second group, the palaeotropic migrants, to arrive and mingle with the flora. Thus the present flora represents an aggregate of different elements with migratory origins reaching back to temperate southern antarctic and northern tropic regions. Superimposed were long periods of isolation, geological pulsations, and the tremendous impact of glaciation.

Fossil History. In recent reviews Oliver (1953, 1955) has recognised three main New Zealand floras.

The Permo-Mesozoic Flora. This flourished during the Jurassic period and was characterised by the general absence of angiosperms and the dominance of ferns and gymnosperms. This first known flora ranged over the whole of the postulated southern continent of Gondwanaland, in which New Zealand now finds a place due to the recent discovery of Permian fossils.

The Cretaceo-Oligocene Flora. This appears after a long gap and includes the first known angiosperms. They were types indicative of a cool climate; sycamores, beeches, oaks and chestnuts. But few of these genera have survived to the present time. The gymnosperm element included species referable to *Araucaria, Ginkgo, Dacrydium* and *Podocarpus.* At first the angiosperm immigrants from the north mingled to give the Cretaceous flora. Increasing rapidly in dominance, species referable to *Nothofagus, Cinnamomum, Acer, Beilschmiedia* and *Hoheria* are recorded from the Upper Cretaceous. By the Oligocene *Melicytus, Carpodetus, Pomaderris* and *Haastia* were added. The last-named is a dicot with banana-like leaves found together with others to which only fossil names can be given.

The Cretaceous was an important period in the history of the flora. During this time the ancestors of many of the present day plants and animals arrived. With land extensions postulated to the south and to the north and fossil elements indicative of both cold and warm climates present, there have been wide interpretations of the origin of the Cretaceo-Oligocene flora.

According to Flemming (1949) post-Jurassic New Zealand has been almost continually archipelagic with elevation and sinking of island groups giving ideal conditions for intense speciation. Couper (1951) saw the early Cretaceous to upper Eocene flora as one characterised by the incoming of angiosperms but with a great assemblage of now extinct conifers also present. Indeed, these conifers must have constituted the dominant forest vegetation, for at every age until then they are by far the most abundant pollen group both in quantity and species. Proteaceae were then more important than at the present time (see Fig. 24).

About the end of the Oligocene a great number of the early angiosperms disappear from the record. There is evidence relating this to a general floristic regression in the southern hemisphere. Climatically this period is related to the onset of the tropical Miocene period in New Zealand (Harris, 1951). There were also marked changes in the pollen records for Australia and South America. McQueen (1951) reports that of 25 plant families present before the Eocene-Oligocene boundary, six are now extinct. Both he and Couper (1953) point out that many Cretaceo-Oligocene fossils recorded in New Zealand are now to be found living only in Australia, Tasmania and New Guinea, where they apparently survived the regression.

With the disappearance in New Zealand of such genera as *Acer, Cinnamomum, Sassafras, Dryandra, Araucaria, Athrotaxis* and others, the flora entered its third phase.

The Miocene-Pliocene Flora. The close of the Eocene sees a sudden disappearance of the conifers and the Miocene forests would appear to have been dominantly broadleaf forests. It is to this period that we can refer for the ancestry of the modern broadleaf forest. The change from the Cretaceo-Oligocene flora to the Miocene flora was undoubtedly a climatic one. Migration routes by land were by this time severed. New Zealand generally is considered to have been isolated from the rest of the world since the late Cretaceous, Boughey (1957). Both Flemming (1957) and Oliver (1953) agree, however, to transoceanic migrations throughout the Tertiary and later, to account for minor peculiarities in the present flora. Oliver saw the last possible connection northward about the Eocene and Flemming agrees to a last pacific pulsation resulting in an extension of land

without continuity as late as the Oligocene. Interchange at this time would have allowed New Zealand to receive an advanced flora and yet not be invaded by mammals and snakes. A modern Malaysian element is not present in New Zealand, and everything points to a subsequent independent evolution of the late Cretaceous plants. The palaeotropic element, never richly endowed generically, has developed in isolation an impressive number of endemic species. Endemic genera in the present vascular flora amount to about 10%, whereas endemic species amount to almost 80%.

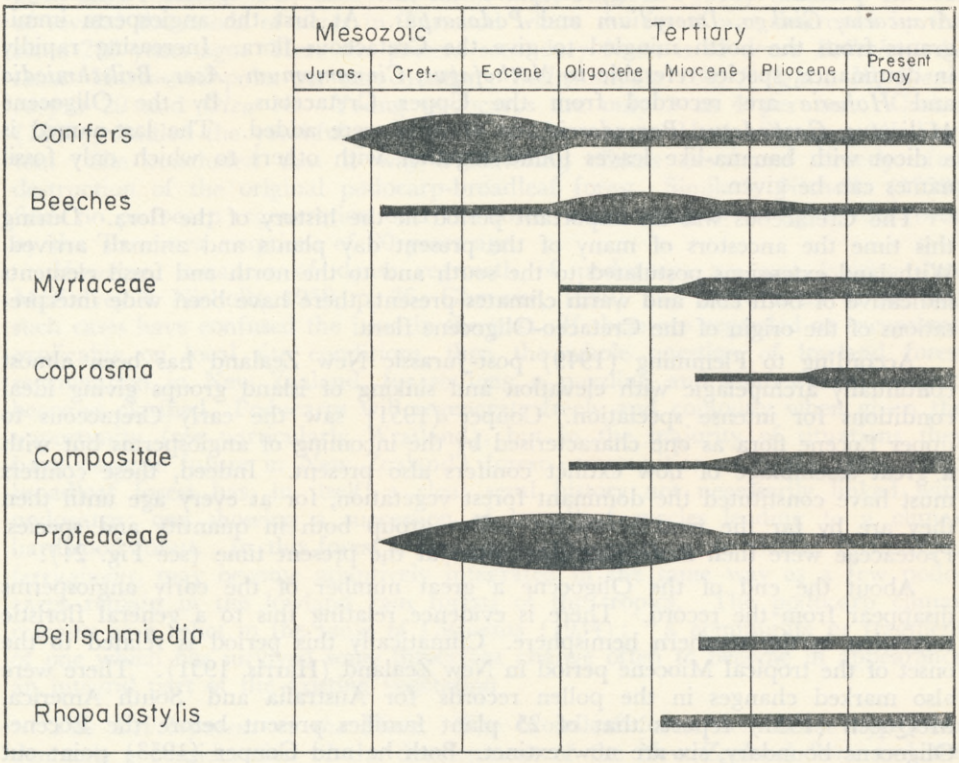

FIG. 24.—Known geological record of some forest species in New Zealand, based on pollen studies from 16 localities, after Couper (1951).

During the Miocene, these earlier immigrants were subjected to a tropical climate, and many of the colder facies disappeared altogether. Couper (1952) suggests a Miocene climate at least 12° F. higher than at present for North Auckland where the fossil *Cocos zelandica* occurs. A number of evergreen broadleaf tree species commonly regarded as of tropical origin, begin their fossil record or show a marked increase during the Miocene period. There is little doubt that the tropical physiognomy which is still to be seen in the New Zealand flora developed during this period. Such features are therefore not due as often implied, to any past continuity with tropical forests or to the direct and recent immigration of tropical plants. They are features which are *autochthonous* in origin. The woody and herbaceous epiphytes, the trailing lianes, the tree stranglers; even the palms and the buttressed and cauliflorous trees of the present New Zealand forest do not belong to representative tropical families or genera. A careful analysis of the floristic, physiognomic and structural features, so long quoted as tropical aspects of the New Zealand lowland forest show them to be

more apparent than real. They represent parallels, not true affinities; epharmonic responses of the regional flora to a past tropical climate.

Although Oliver (1953) held that some of the Jurassic flora may have survived, positive relationship for the modern podocarps can be said to go back only as far as the Cretaceo-Oligocene flora. While most of this flora shows a northern affinity with tropical Malaysia there appears little doubt that New Zealand was also, at this time, open to receive southern migrants. Numerous writers from Skottsberg (1925) to Croizat (1952) have continued the theme of a southern origin for much of the New Zealand flora in a warm Antarctica. Florin (1940) accepts the origin of a distinct southern gymnosperm flora. These southern gymnosperms are given a northward migration route into the Pacific by Setchell (1935) while Guppy (1903-09) suggested that the present podocarps in Fiji are relics, now overwhelmed by tropical lowland broadleaf immigrants which arrived at a later date. Buchholz and Gray (1948) in their taxonomic studies related the New Zealand podocarps to stock evolving in southern regions. Cranwell (1959) has recently re-emphasised the Antarctic centre of origin. Cretaceous, and probably lower Miocene deposits from Seymour Island reveal a dominance of conifers and *Nothofagus* beeches. For some of these early migrations one may evoke the continental drift hypothesis which received recent attention by Sewell (1956) and, with special reference to Australasia, by Good (1957). Table I summarises the history of the New Zealand flora.

Glacial and Post-Glacial Forest History. Post Miocene was a period of cooling from the tropical climate, and this continued until its culmination in the Pleistocene glaciations. Pliocene, Pleistocene and post-Pleistocene history becomes a record of the flora. However, the Pliocene-Pleistocene forests have, unfortunately, left little record of their exact nature. Couper and McQueen (1954), in their fossil microspore studies indicate local fluctuations throughout the period between *Nothofagus* and podocarp forests. Most of their records relate to the South Island and here it is known that these fluctuations continued into the Holocene, see Cranwell and von Post (1936).

For the Waikato in the North Island, Couper and Harris (1960) report an interesting microfossil vegetation covering the upper Pliocene to the lower Pleistocene. Apparently their upper Pliocene microfossils represent an extension of the tropical Miocene vegetation as, apart from many warmth-demanding dicots of present genera, there are pollens of Bombacaceae, Sapindaceae, Proteaceae and Ephedraceae and abundance of *Nothofagus* of the *brassii* (New Guinea) type. Living representatives of such are now found only in subtropical and tropical regions. The record shows a sudden disappearance of these tropical elements and in the lower Pleistocene it is *Nothofagus* of the *fusca* type which dominates together with podocarps. Similar contemporary vegetation successions are now known from a number of localities in New Zealand. As recent peats in the Waikato area reveal a dominant podocarp forest there is reason to believe that such forests have been continuous with those from the Pleistocene.

Conditions prevailing at the time of the first major glacial period have been described by Willett (1950). He has estimated that the Pleistocene regional snowline came down generally 3,500ft lower than at present, with a mean reduction in temperature of 6° C. The Southern Alps and the whole of Westland were at the time covered with glacial ice and surrounding this were extensive areas of tundra and steppe. In fact, forest was virtually eliminated from the South Island. In the North Island there were small areas of ice with their periglacial zones, but the larger part of the North Island remained in forest. Very little is known of the detailed nature of these forests, or indeed those which were present throughout the whole period of glacial advance and retreat with intervening warmer

Table I.—CLIMATE AND VEGETATION IN THE GEOLOGICAL RECORD IN NEW ZEALAND.

	Period	Climate	Flora	Forest History
QUATERNARY	Recent	Temperate Warming	Modern. Known mainly from micro-spore studies.	Post-glacial ascendancy of temperate broadleaf trees. Recolonisation by gymnosperm forests.
	Pleistocene	Cold (glaciation)	Modern flora.	Elimination of many warm-loving genera.
TERTIARY	Pliocene Miocene	Cooling Tropical	Mio-Pliocene flora. Basis of the present flora. Known only from the end of the Miocene. Many genera of tropical nature which are now extinct in N.Z.	Broadleaf forests dominant with conifers in retreat.
	Oligocene	Cooler	Early angiosperm of the Cretaceo-Oligocene (Sycamores, Oaks), which died out in Oligocene. Podocarps identified.	Possible late northern land extensions. Rising abundance of angiosperms.
MESOZOIC	Late Cretaceous	Cool	Long gap in the fossil record.	Last land connections severed. N.Z. isolated.
	Early Cretaceous	Warm		
	Jurassic	Warm	Early gymnosperm Permo-Mesozoic flora (Ferns, cycads, conifers.) Mostly from Jurassic.	
	Triassic Permian	Arid Cold (glaciation)		

periods. Many of the tropical broadleaf species of the Miocene were eliminated. Such fossil genera as *Cocos* and *Haastia* died out and others were decimated of all but their most hardy species.

Unfortunately the fossil record fails as yet to contribute to the major part of the Miocene, but there is little doubt that we should find a wealth of now extinct species belonging to present-day broadleaf genera with but a single to a few endemic species. One could expect to find fossil representation of genera now existing only in the refugeum of New Guinea's montane forests, Robbins (1961).

Post-glacial Forests. It has been widely held that the dominant post-glacial forests of the North Island were of *Nothofagus* (Willett, 1950; Nicholls, 1956). However, although *Nothofagus* is prominent in the available fossil record, there is thus far no evidence of vast post-glacial beech forests in the North Island. *Nothofagus* forest was contemporary, but not necessarily at the same altitudinal level as the podocarp forest. With the timber line lowered to 1,500ft, it follows that most of the forests were of a montane type, and these may well have been dominated by *Nothofagus*. True lowland podocarp forest persisted only at altitudes below 500ft. The greater part of the present podocarp-broadleaf forests lie above 1,500ft, and hence they must represent post-glacial colonising forests which replaced the montane forests and indeed much of the periglacial steppe-tundra. Hence while beech forests may have extended their area during the Pleistocene they were later largely replaced by vast podocarp forests in the North Island. It is contended that the present podocarp element within the broadleaf forest is continuous with this period. Only in Westland is this post-glacial podocarp relic still dominant. This was the site of a vast piedmont glacier and a subsequently prolonged tundra stage which has only lately been recolonised by pioneer gymnosperm forests.

Younger still are the dense podocarp forests of the central plateau which resulted from a different catastrophe. Their advantage, however, is but a temporary respite, and even now they are being ousted by broadleaf forests. Perhaps it is of more than passing interest to note that broadleaf invasion of the exotic pine plantations on the volcanic plateau is already providing a problem to foresters (Henry, 1954). Everywhere then, New Zealand's podocarp forests are in retreat. Eventually broadleaf forests will dominate again as in Miocene times. Thus may we interpret more fully Cockayne's observation (1928a, p. 21) that the podocarps are "a remnant merely of ancient conifer forests which have been in the process of gradual extinction by certain broad-leaved dicotylous trees—a process of extreme slowness".

APPENDIX

Explanation of symbols used in profile diagrams:—

Ae—*Alectryon excelsum* Gaertn.
Ar—*Aristotelia racemosa* Hook. f.
Bt—*Beilschmiedia tawa* Benth. & Hook. f.
Bta—*Beilschmiedia tarairi* Benth. & Hook. f.
Ca—*Coprosma australis* (A. Richard) Robinson.
Cd—*Cyathea dealbata* Swartz. (treefern).
Cs—*Carpodetus serratus* Forst.
Ct—*Coprosma tenuifolia* Cheesem.
Dc—*Dacrydium cupressinum* Soland.
Ds—*Dysoxylum spectabile* Hook. f.
Dsq—*Dicksonia squarrosa* Swartz (Treefern).
Ed—*Elaeocarpus dentatus* Vahl.
Gen—*Geniostoma ligustrifolium* A. Cunn.
Gl—*Griselinia littoralis* Raoul.
Ha—*Hedycarya arborea* Forst.
Hp—*Hoheria populnea* A. Cunn.
Hs—*Hemitelia Smithii* (Treefern).
Ke—*Knightia excelsa* R. Br.
Ln—*Laurelia novae-zelandiae* A. Cunn.
Mb—*Myrtus bullata* Soland.
Met.r—*Metrosideros robusta* A. Cunn.
Mu—*Metrosideros umbellata.*
Mr—*Melicytus ramiflorus* Forst.
Na—*Nothopanax arboreum* Seem.
Ne—*Nothopanax edgerleyi* Harms.
Ol—*Olea lanceolata* Hook. f.
Or—*Olearia rani* (A. Cunn.).
Pc—*Pennantia corymbosa* Forst.
Pd—*Podocarpus dacrydioides* A. Rich.
Pf—*Podocarpus ferrugineus* D. Don.
Ph—*Podocarpus hallii* T. Kirk.
Pm—*Paratrophis microphylla* Cockayne.

Ps—*Podocarpus spicatus* R. Br.
Ps a—*Pseudowintera axillaris*
Psc—*Pseudowintera colorata*
Pt—*Podocarpus totara* D. Don.
Qa—*Quintinia acutifolia* T. Kirk
Rs—*Rhipogonum scandens* Forst. (Palm).
Sa—*Suttonia australis* A. Rich.
Sd—*Schefflera digitata* Forst.
Ss—*Suttonia salicina* Hook. f.
Wr—*Weinmannia racemosa* Linn. f.
Ws—*Weinmannia sylvicola* A. Cunn.

REFERENCES

AUBREVILLE, A., 1938. La foret coloniale: Les forets de l'Afrique occidentale francaise. *Ann. Acad. Sci. colon.,* Paris 9: 1–245.

BEARD, J. S., 1944. Climax vegetation in tropical America. *Ecology.* 31.1; 89–99.

BIELESKI, R. L., 1959. Factors affecting growth and distribution of kauri (*Agathis Australis* Salisb.) Pt. III. *Aust. J. Bot.,* 7.3: 279–294.

BOUGHEY, A. S., 1957. The origin of the African flora. Inaug. lect. Univ. Rhodesia & Nyassaland. *O.U.P.,* pp. 48.

BUCHHOLZ, J. T., and NETTA E. GRAY, 1948. A taxonomic revision of *Podocarpus. Jour. Arnold Arbor.* 29: 49–63.

CAMERON, R. J., 1954. Mosaic or cyclical regeneration in North Island podocarp forest. *N.Z. Jour. For.* 6.5: 55–64.

CHAVASSE, C. G. R., 1954. Potentialities for indigenous and exotic forestry in Westland. *N.Z. Jour. For.* 7.1: 34–49.

CLEMENTS, F. C., 1934. The relict method in dynamic ecology. *Jour. Ecol.* 22: 39–68.

COCKAYNE, L., 1928. *The Vegetation of New Zealand.* (2nd Ed.) Die Vegetation der Erde 14. Englemann, Leipzig.

——— and E. P. TURNER, 1928a. *The Trees of New Zealand.* State For. Pub. Wellington.

COUPER, R. A., 1951. Evidence from earlier times. *N.Z. Sci. Rev.* 9. 1 and 2: 12–14.

——— 1952. The spore and pollen flora of the Cocos-bearing bed, Manonui, North Auckland. *Trans. Roy. Soc. N.Z.* 79: 340–348.

——— 1953. Distribution of Proteaceae, Fagaceae, and Podocarpaceae from the Cretaceous to the Oligocene. *N.Z. J. Sci. Tech. B 35*: 247–250.

——— and W. F. HARRIS, 1960. Pliocene and Pleistocene plant microfossils from drill-holes near Frankton, N.Z., *N.Z. J. of Geol. & Geophysics.* 3.1: 15–21.

——— and D. R. MCQUEEN, 1954. Pliocene and Pleistocene plant fossils of N.Z. and their climatic interpretation. *N.Z. J. Sci. Tech.* B. 35: 389–420.

CRANWELL, LUCY M., and L. VON POST, 1936. Post-Pleistocene pollen diagrams from the southern hemisphere. I. New Zealand. *Geograf. Annaler.* H. 3.4: 8–374.

CRANWELL, LUCY M., 1959. Fossil pollen from Seymour Island, Antarctica. *Nature.* 184.4701: 1782–1785.

CROIZAT, L., 1952. *Manual of Phytogeography.* The Hague. pp. 557.

CROKER, BARBARA H., 1953. Forest regeneration in the Western Hutt hills, Wellington. *Trans. Roy. Soc. N.Z.,* 81.1: 11–21.

DAVIS, T. A. W., and P. W. RICHARDS, 1933. The vegetation of Moraballi Creek, British Guiana. *Jour. Ecol.* 21: 35–84.

DU RIETZ, E., 1930. Classification and nomenclature of vegetation. *Svensk. Bot. Tidskr.* 24. H. 4.

FERGUSSON, G. T., and T. A. RAFTER, 1953. New Zealand C14 age measurements. *N.Z. J. Sci. Tech.* B. 35: 127–128.

FLEMMING, C. A., 1949. The geological history of New Zealand. *Tuatara.* 2: 72–90.

——— 1957. Transtasman relationships in natural history. In "*Science in N.Z.*" Hdbk. for 32nd ANZAAS conf. Reed, Dunedin.

FLORIN, R., 1940. In "*K. Sv. Vet. Handl.*" 19.2: 28.

GRANGE, L. I., and N. H. TAYLOR, 1932. N.Z. *D.S.I.R. Bulletin No. 32*: 21–35.

GOOD, R., 1957. Some problems of southern floras with special reference to Australasia *Aust. J. Sci.* 20.2: 41–44.

GRANT, P. F., 1949. The geography and ecology of Saltwater forest, S.F. 40, Westland. Unpub. rec. N.Z. Forest Service.

GUPPY, H., 1903. *The observations of a naturalist in the Pacific.* Vol. I. Fiji. MacMillan, London.

HARRIS, W. F., 1955. Progress report on pollen statistics from Pyramid Valley swamp. *Rec. Canterbury Mus.* 6.4: 279–290.

——— 1950. Climate relations of fossil and recent floras. *Tuatara.* 3.2: 53–65.

——— 1951. Unravelling forest history in New Zealand. *N.Z. Sci. Rev.* 9.1 and 2: 5–9.

HENRY, E. J., 1954. The development of native vegetation on pumice country and its relationship with exotic pine forests. *N.Z. Jour. For.* 7.1: 79–82.

Hewetson, C. E., 1956. A discussion on the "climax" concept in relation to the tropical rain and deciduous forest. *Emp. For. Rev.* 35.3: 274–291.
Hinds, H. V., and J. S. Reid, 1957. *Forest trees and timbers of New Zealand.* N.Z. For. Ser. Bul. No. 12, Wellington. pp. 211.
Holloway, J. T., 1946. Forest associations of the Longwood Range, Southland. *N.Z. Jour. For.* 5.3: 199–209.
——— 1946a. Unpub. National Forest Survey, Forestry School course. N.Z. Forest Service records.
——— 1954. Forests and climates in the South Island of New Zealand. *Trans. Roy. Soc. N.Z.,* 82.2: 329–410.
——— 1954a. Commentary on Cameron, R. J. (1954). *N.Z. Jour. For.* 6.5.
——— 1959. In *A descriptive atlas of New Zealand.* Govt. Printer, Wellington.
Jones, E. W., 1955–56. Ecological studies on the rain forest of southern Nigeria. Pts. I and II. *Jour. Ecol.* 43.2: 564–594; and 44.1: 83–117.
Masters, S. E., and J. T. Holloway and P. J. McKelvey, 1957. The National Forest *Survey of New Zealand, 1955.* Vol. 1. The indigenous forest resources of N.Z., pp. 107. Govt. Printer, Wellington.
McKelvey, P. J., 1953. Forest colonisation after recent volcanicity at West Taupo. *N.Z. Jour. For.* 6.5: 435–448.
——— and J. L. Nicholls, 1957. A provisional classification of North Island forests. *N.Z. Jour. For.* 7.4: 84–101.
——— 1959. The indigenous forest types of North Auckland. *N.Z. Jour. For.* 8.1: 29–45.
Nicholls, J. L., 1956. The historical ecology of the indigenous forest of the Taranaki Upland. *N.Z. Jour. For.* 7.3: 17–34.
Oliver, W. R. B., 1953. Origin of the New Zealand Flora. *Proc. 7th Pacific Sci. Congr.* 5: 131–146.
——— 1955. History of the flora of New Zealand. *Sv. Bot. Tidskr.* 49. 1 and 2: 9–18.
Poole, A. L., 1937. A brief ecological survey of the Pukekura State Forest, South Westland. *N.Z. Jour. For.* 4.2: 78–85.
Richards, P. W., 1952. *Tropical rain forest.* Camb. Univ. Press, pp. 450.
——— and A. G. Tansley asd A. S. Watt, 1940. The recording of structure, lifeform, and flora of tropical forest communities as a basis for their classification. *Jour. Ecol.* 28: 224–239.
Robbins, R. G., 1958. Direct effect of the 1855 earthquake on the vegetation of the Orongorongo Valley, Wellington. *Trans. Roy. Soc. N.Z.,* 85.2: 205–212.
——— 1959. The use of the forest profile diagram in rain forest ecology. *Jour. Biol. Sci.* (Bombay) 2.2: 53–63.
——— 1961. The montane vegetation of New Guinea. *Tuatara* 8. 3: 121–133.
Scurfield, G., 1956. Note on experimental ecology and the uses of a biological flora. *Vegetatio.* 7.1: 3–7.
Setchell, W. A., 1935. Pacific floras and Pacific paleogeography. *Am. Nat.* 69: 289–310.
Seymour-Sewell, R. B., 1956. The continental drift theory and the distribution of Copepoda. *Proc. Linn. Soc.* London. 166. 1 and 2: 149–177.
Skottsberg, C., 1925. Juan Fernandez and Hawaii, a phytogeographic discussion. *Bishop Mus. Bul.* No. 16. Hawaii.
Watt, A. S., 1947. Pattern and process in the plant community. *Jour. Ecol.* 35: 1–22..
Willett, R. W., 1950. The N.Z. Pleistocene snowline, climatic conditions and suggested biological effects. *N.Z. J. Sci. Tech.* B 32: 18–48.

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